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THE EMERGENCE OF DARWINISM

By Sir JULIAN HUXLEY, F.R.S.

(*Being the Darwin-Wallace Memorial Lecture delivered at the Inaugural Meeting of the XVth International Congress of Zoology on* 16*th July*, 1958.)

TO-DAY we celebrate the centenary of an outstanding event in the history of science—the birth of Darwinism or evolutionary biology, initiated by the joint contribution of Charles Darwin and Alfred Russel Wallace to The Linnean Society of London, announcing their independent discovery of the principle of natural selection.

I say Darwinism because not only did Darwin have priority in conceiving that evolution must have occurred, and could only have occurred through the mechanism of natural selection, but also contributed far more than Wallace, or indeed than any other man, to the solution of the problem and the development of the subject. I shall therefore speak almost entirely about Darwin and Darwinism, endeavouring to bring out facts and ideas which illuminate Darwin's unique role in the history of our science.

Charles Darwin has rightly been described as the Newton of biology : he did more than any single individual before or since to change man's attitude to the phenomena of life, and to provide a coherent scientific framework of ideas for biology, in place of an approach in large part compounded of hearsay, myth and superstition. He rendered evolution inescapable as a fact, comprehensible as a process, all-embracing as a concept.

His industry was prodigious. His published books run to over 8000 printed pages, and contain, on my rough estimate, at least 3,000,000 words. His scientific correspondence must have reached similar dimensions, and his contributions to scientific journals comprise well over 400 pages.

The range of subjects with which he dealt, often as an initiator and always magisterially, was equally remarkable. Let us first recall that at the outset of his career he was more of a geologist than a biologist, that his first scientific works, on Coral Reefs and on the Geology of South America, dealt with geological subjects, and that the only professional position he ever occupied was that of Secretary to the Geological Society. Later, he dealt with the taxonomy and biology of that 'difficult' group of animals, the barnacles or Cirripedes, in its entirety; with the principles and practice of classification; with the evidences for evolution; the theories of natural and sexual selection and their implications; the descent of man, including the evolution of his intellectual, moral and æsthetic faculties; the emotions and their expression in men and animals; geographical distribution, domestication, variation in nature and under domestication, the effects of self- and cross-fertilization (or, as we should now say, in- and out-breeding) and various remarkable adaptations for securing cross-fertilization, the movements of plants, insectivorous plants, and the activities of earthworms.

Not only is he the acknowledged parent of evolutionary biology, but is also prominent among the founding fathers of the sciences we now call ecology and ethology.

Above all, he was a great naturalist, in the proper sense that he was profoundly interested in observing and attempting to comprehend the phenomena of nature, though at the same time he managed to keep abreast of pure scientific advance in the fields which concerned him, such as general botany, embryology, palæontology, biogeography, taxonomy, and comparative anatomy, as well as with the activities both of professionals and amateurs in what we should now call plant and animal breeding.

He had an inborn passion for natural history, which showed itself from early childhood. Later, like most true naturalists, besides being motivated by intellectual interest, he was deeply moved by the wonder and beauty of nature. As a young man, he found an 'exquisite delight in fine scenery',[1] and enjoyed exploring wild and strange country.

The combination of passionate and deep emotion appears vividly in the notes he made on his first experience of the tropical rain-forest: 'Twiners entwining twiners—tresses like hair—beautiful lepidoptera—Silence—hosannah—frog habits like toad—slow jumps'. 'Sublime devotion the prevalent feeling.' And a little later, 'Silence well exemplified. . . . Lofty trees, white boles . . . So gloomy that only shean [sic] of light enters the profound. Tops of the trees enlumined'.[2]

I may perhaps note that this last entry was made, not in the remote depths of the great Amazonian forest as one might expect, but close to Rio, at Botofogo, whose beach is now bordered by luxury hotels and crowded with bathing beauties. However, though roads have robbed the forest behind the beach of its primal virginity, it is otherwise untouched, and in its recesses one can still recapture some of Darwin's feelings.

Another characteristic of Darwin was his extraordinary diffidence, coupled with a passion for completeness and a reluctance, so extreme as to appear almost pathological, to publish to the world his ideas on the controversial subject of evolution before he had buttressed his arguments with a body of evidence which would overwhelm opposition by its sheer vastness. It has been suggested that these traits in Darwin's character, and also the constant ill-health from which he suffered after his marriage in 1839, were neurotic symptoms springing from unconscious conflict or emotional tension, and that this in its turn was first generated by Darwin's ambivalent attitude to the dominating and domineering figure of his father, Robert Darwin.[3]

While not necessarily accepting this interpretation in its entirety, there seems no doubt that his ill-health was in part what psychiatrists now call an escape mechanism, and was fostered by the devotion of his wife, who became the ideal sick-nurse, as Darwin became the ideal patient; nor that his reluctance to commit himself publicly and in print to belief in the mutability of species and in evolution by natural causes, sprang ultimately from some unacknowledged inner conflict which was partly rooted in his relations with his father. It was his father who took him away from school early because he thought he was idle and doing no good; who decided first that he should study medicine, and then, when it was clear that Charles disliked the prospect of becoming a physician, sent him to Cambridge to study for the Church, another profession for which he had no inclination or aptitude; and whose strong opposition to Charles accepting the post of naturalist on the *Beagle* nearly robbed the world of its greatest biologist[4]. He clearly deplored Charles' intense (and apparently innate) devotion to nature and natural history, which was manifested in the pursuits of his childhood and youth, from beetle-collecting to shooting and geologizing in the field. Furthermore, his father was a man of decided opinions, very autocratic with his children, and probably hostile to the whole idea of evolution. In his autobiography Charles states that he never heard the idea of evolution favourably mentioned until he had gone as a medical student to Edinburgh: this at least indicates that it was not discussed in the Darwin home. In any case, what could be more symptomatic of a guilt-complex than Darwin's confession, in a letter to Hooker early in 1844, that to assert that species are not immutable is 'like confessing a murder'![5] If he felt like this, it is little wonder that he kept on putting off the public statement of his views.

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[1] *Autobiography*, L. and L., **1**; 101. *Note.*—In the biographical references, *L. and L.* denotes *The Life and Letters of Charles Darwin*, edited by F. Darwin, 3 vols, 3rd edition, 1887; *Origin* denotes *The Origin of Species* by Charles Darwin, reprint of the 6th edition (1872) with preface by G. R. de Beer, Oxford University Press, 1956; *Descent of Man* denotes *The Descent of Man and Selection in Relation to Sex*, by Charles Darwin, reprint of the 2nd edition (1874), John Murray, 1922; *Nora Barlow* denotes *The Autobiography of Charles Darwin*, the first complete version, edited and annotated by Nora Barlow, Collins, 1958.

[2] *Charles Darwin and the voyage of the Beagle.* Ed. Nora Barlow, Pilot Press, 1945, pp. 162–165.

[3] See e.g. *Biology and Human Affairs* (1954), **20**; p. 1; R. Good, *ibid.*, p. 10. Also Nora Barlow, p. 240 f.

[4] See Nora Barlow, p. 226f.

Furthermore, the conflict must have been sharpened by his marriage, for his deeply religious wife was opposed to all unorthodox views. In any case, his chronic ill-health did not begin until after his marriage.[6]

His extreme diffidence about the merits of his work (clearly another symptom of inner conflict) is illustrated by a letter of 27 August 1859 to his publisher, John Murray, about the 'little work'—as he called the *Origin of Species*—which he was then preparing. 'I feel bound (he wrote) for your sake and my own to say in clearest terms that if after looking over part of my MS. you do not think it likely to have a renumerative sale I completely and explicitly free you from your offer.'[7]

It is worth while retelling the salient facts of the story. During the voyage of the *Beagle*, probably towards the end of 1835, he had become convinced that species could not be separate immutable creations. In 1837, soon after his return to England, he started a series of notebooks on the 'transmutation of species', in the full consciousness that this would imply large-scale evolution and the common ancestry of all organisms, including man. He soon realized the efficacy of selection in creating new varieties and races of domestic animals and plants, but was unable to see how it could operate in nature. Then, late in 1838 he 'happened to read for amusement *Malthus* on *Population*'—I quote his own revealing phrase—and the idea of natural selection immediately flashed upon him. 'Here then' he continued, 'I had at last got a theory to which to work.' This vivified all his subsequent thinking: for do not let us forget that Darwin combined inductive and deductive method in a remarkable way. He was never interested in facts for their own sake, but only in their relevance to some hypothesis or general principle.[8] But when he had discovered some satisfactory general principle, he proceeded to deduce the most far-reaching conclusions from it. This is particularly evident, as will appear later, with the principle of natural selection; but it is also true of his treatment of uniformitarianism and the principle of continuity, of sexual selection, and of biological adaptation.

This is perhaps the place to stress another aspect of Darwin's mind. Although his laborious patience in the collection and synthesis of factual evidence has rarely been rivalled (he himself called his mind 'a kind of machine for grinding general laws out of large collections of facts'[9]), yet sudden intuition was responsible for some of his most important discoveries of principle, notably natural selection and the explanation of biological divergence—a valuable reminder of the fact that imagination as well as hard work is essential for scientific comprehension.

But I must return to my story. In spite of this illuminating discovery, his reluctance to commit himself was such that not until four years later did he 'allow himself the satisfaction' (again a revealing phrase) of putting his ideas on paper; and then only by 'writing out in pencil a very brief abstract' of his theory and the evidence for it.[10]

Two years later, in 1844, he enlarged this into an 'Essay'. As a matter of fact, this so-called Essay was a sizeable book of 230 pages, covering almost the same ground as the *Origin,* and more than adequate as an exposition of the whole subject.[11] Yet he still procrastinated, and continued to procrastinate for 14 further years. He showed the Essay to no one but Lyell, and discussed his evolutionary ideas only with him and a few intimate colleagues, notably Hooker. He continued with the interminable collection of facts, until finally, urged on by Lyell and Hooker, he began in 1856 to write a monumental work on the subject.

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[5] L. and L., **2**. This was some eight years after he had become personally convinced of the fact!

[6] The two and a quarter years in London before his marriage he records as the most active he ever spent, marked only by occasional spells when he felt unwell (*Autobiography*, L. and L., **1**; 67).

[7] Quoted by kind permission of John Murray, Ltd.

[8] See Nora Barlow, pp. 157–164.

[9] *Autobiography*, L. and L., **1**; 101.

[10] *The Foundations of the Origin of Species*, a sketch written in 1842 by Charles Darwin; edited by Francis Darwin, Cambridge, 1909.

Here I must pay tribute to Alfred Russel Wallace. I wish I had more space to set forth his great contribution to evolutionary biology. He laid the foundations of zoogeography, and his notable works on the subject—*the Geographical Distribution of Animals* and *Island Life*—can still be read with profit, as can those on tropical natural history in general—*Tropical Nature* and *The Malay Archipelago.* He was the first to make a comprehensive analysis of cryptic adaptations, he contributed materially to the study of mimicry, and originated the theory of warning coloration. He made many original contributions to the species problem, and in 1855 had published a paper ' On the Law which has regulated the Introduction of New Species ' (*Ann. Mag. Nat. Hist.*, 1855, p. 184), which showed that he believed in the evolution of new species from old, and led to Darwin entering into correspondence with him.

But not only was he a great naturalist, not only did he independently discover the principle of natural selection, but by doing so he forced Darwin into publication. If it had not been for Wallace's attack of malarial fever in Ternate and his impulsive temperament, the *Origin of Species* would never have been published in 1859. Ever since 1855, when he had become convinced that evolution had occurred, the question of *how* changes of species could be brought about was constantly in his thoughts, but he never succeeded in thinking the problem out. The fever, by setting him free from his daily routine of practical detail, permitted his roving mind to discover the principle of natural selection (as with Darwin, in a sudden flash of intuition, and also as a result of reading Malthus and Lyell some time previously) ; and his temperament, the very opposite of Darwin's, led him to write down his ideas that same evening, to elaborate them during the next two days, and then send them straight off to Darwin for his opinion. The first result, after much heart-searching on Darwin's part and the firm intervention of Lyell and Hooker, was the joint announcement of Darwin's and Wallace's views to The Linnean Society of London on 1 July 1858, and their subsequent publication in the Society's Journal. The second and much more important result was the publication of the *Origin of Species.* Strongly pressed by Lyell and Hooker, in September 1858, Darwin started ' abstracting ' (his own word) his huge incomplete work, and finished the book in just over 13 months. Although in his Autobiography he still called it ' only an abstract ', he acknowledged that it was ' no doubt the chief work of my life ', and this is certainly true.

But for Wallace and his fever, Darwin would assuredly not have overcome his resistance to speedy publication, and would have continued working on ' the MS. begun on a much larger scale '. In 1858 he envisaged its completion ' at the soonest ' by 1860. But we can be sure that his inhibitions over coming into the open, which were transmuted into perfectionist dreams of completeness (' I mean to make my book as perfect as ever I can ', he wrote as late as February 1858[12]), would have prevented him from publishing for a much longer time—perhaps five, perhaps even ten years.

He himself said that the book would have been ' four or five times as large as the *Origin* '—which would mean at least 2500 pages, and over three-quarters of a million words!—and that very few would have had the patience to read it.[13] It would, indeed, have been almost unreadable, and the forceful flow of argument, so well manifested in the *Origin*, would have been lost in the sands of over-abundant fact. Biology certainly owes a great deal to Wallace.

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[11] Reprinted with the sketch of 1842, in C. Darwin & A. R. Wallace, *Evolution by Natural Selection,* Ed. G. R de Beer, Cambridge, 1958.

[12] L. and L., **2** ; 110.

[13] *Autobiography,* L. and L., **1** ; 88.

Nor must we forget Lyell. He was the chief source of encouragement to Darwin in his evolutionary work after his return to England, and was mainly instrumental in persuading him to publish his ideas together with Wallace's paper in 1858. We know that his *Principles of Geology* influenced Wallace more than any other book. Above all, his great work demonstrating that slow geological change had occurred as a result of existing physical causes prepared the ground for the idea of biological evolution by natural means. As T. H. Huxley wrote in 1887, he was 'the chief agent in smoothing the path for Darwin'.

Biology also owes a good deal to Darwin's caution, exaggerated though this was. If Darwin had rushed into print in 1838 with a brief and bare account of his conclusions, they would have been still-born. The idea of evolution needed heavy reinforcement with facts, and the idea of natural selection had to be thoroughly worked out in all its implications. Even though the *Essay* of 1844 went a long way towards satisfying these requirements, its immediate publication would not, I am sure, have been nearly so effective as was that of the *Origin* 15 years later. This is partly owing to Darwin's enlargement of his evidence and improvement of his argument, but also to the 'pre-adaptation' of opinion of which Dr Harrison Matthews writes, the increased interest of biologists in evolution and their increasing readiness to discuss it, as well as to the appearance on the biological stage of younger men, like Wallace, Alfred Newton, and especially Huxley, ready to be persuaded and become forceful champions of the new and revolutionary ideas.[14] The best time for Darwin to publish was, I would say, between 1855 and 1860.

Above all, delay in publication gave Darwin time to look at every aspect of his enormous subject, to think out its many implications, and to meet all possible objections. The result was extremely impressive, and far more convincing than any brief sketch, however brilliant, or any speculative picture, such as those drawn by Erasmus Darwin or Lamarck.

The last paragraph of the *Origin* has often been quoted: I quote it here once again, as admirably illustrating this close-reasoned comprehensiveness of Darwin's work :—'It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of of the conditions of life, and from use and disuse; a ratio of increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, ... that, whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are, being evolved.'

It is interesting to pursue the question of timing onto a more speculative plane, and ask ourselves what would have happened to Darwin if he had been born a century earlier or a century later. I would guess that if he had been born in 1709 he might well have become a good amateur naturalist, rather after the pattern of his grandfather

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[14] Newton was converted by the joint Darwin-Wallace paper of 1858. 'Never shall I forget the impression it made on me', he wrote; 'Herein was contained a perfectly simple solution of all the difficulties that had been troubling me for months past' (Nora Barlow, p. 157). Otherwise the Linnean paper seems to have fallen rather flat, and it was reserved for the *Origin* in 1859 to produce a major effect.

Erasmus, one who would, perhaps, have indulged in some interesting speculations on natural history, but would not have been likely to make any major discoveries or to exert any important influence on scientific or general thinking. If he had been born in 1909, he might at most, I would hazard, have achieved some eminence as a professional ecologist. In the one case the time was unripe, in the other over-ripe.

Kroeber has demonstrated that the effective manifestation of genius requires not only exceptional individual talent, but depends also on the circumstances and sometimes the accidents of place and period; nowhere is this better illustrated than in the person of Darwin. First of all, the scientific and intellectual atmosphere was propitious. The time was just ripe for the tying together of the facts of geology and biology by the unifying principles of evolution. Then, as a boy and young man, Darwin was able to indulge his early taste for natural history; later, his financial independence enabled him to devote himself entirely to his own chosen work, and his invalidism prevented him from wasting time and energy in a round of social engagements and scientific meetings; as an Englishman, he quickly came into contact with the ideas of Malthus, Lyell and Hooker, which were so decisive for his thought, and with Huxley, who was so important in spreading his doctrines; above all, he had the luck to go as naturalist on the *Beagle*.

Two circumstances of the voyage seem to have been of outstanding importance. First, he was able to study natural history, in its geological as well as in its biological aspects, on a continental scale, and so to appreciate the overall pattern of the fauna and flora, and also their gradual transitions and modifications of detail in relation to changing conditions of time and place. This forced him to think along broad lines, in terms of continuity and gradual evolutionary change, in a way that would hardly have been possible if he had stayed at home. In similar fashion the small extent but great geological variety of Britain prevented its scientists grasping the general principles of soil science, while the great expanses and broad zonation of the Russian landscape facilitated or even forced their recognition by Soviet pedologists.

The other decisive circumstance was the *Beagle's* visit to the oceanic archipelago of the Galapagos. Oceanic archipelagos are rare natural laboratories, in which enquiring and receptive minds can find a demonstration of evolution and how it operates in practice. Darwin's mind was both enquiring and receptive: it seems clear that his experiences here finally crystallized his thought and convinced him that evolution was a fact.

Here biology must acknowledge its very real debt to Darwin's uncle Josiah Wedgwood. Robert Darwin's objections to Charles accepting the post of naturalist on the *Beagle* were so strong (and his influence on his son so powerful) that Charles, though eager to accept, wrote to refuse the offer. And it was only his uncle's intervention that persuaded his father to withdraw his objections.[15]

Robert Darwin seems to have taken a rather poor view of Charles's abilities and character. In fact, however, these must already have been impressive at the age of 22. They impressed Henslow and Sedgwick at Cambridge; the Hydrographer to the Navy, in a letter to Captain Fitzroy, his future commanding officer, speaks of him as 'full of zeal and enterprise and having contemplated a voyage on his own account to South America'; and Captain Fitzroy himself wrote to the Hydrographer on 15 August 1832, that 'Mr. Darwin is a very superior young man, and the very best that could have been detailed for the task.'[16]

But I must return to my central theme. Whatever the contribution of others, Darwin stands out as the prime author and pre-eminent figure of the biological revolution. Wallace himself fully recognized this. It was he who first called Darwin the Newton of Natural History (or Biology, as we should say to-day), and coined the term *Darwinism* as the title of his own book on evolution. The evidence and the arguments marshalled by Darwin in the *Origin* were decisive in persuading leaders of scientific thought like Huxley and Hooker that evolution had occurred and that it was based on a natural and scientifically intelligible mechanism.

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[15] See Nora Barlow, p. 226f.

[16] These two letters I am enabled to quote by the courtesy of the present Hydrographer, Rear-Admiral Collins.

Furthermore, his inhibitions over publication disappeared with the appearance of the *Origin*, and he proceeded to develop various aspects of the subject with remarkable speed and energy. Twenty-two years elapsed between his opening his notebooks on the transmutation of species and the publication of the *Origin*, and 14 years between the writing of the *Essay* and the appearance of the joint paper with Wallace. In the 14 years after 1859 he published three truly major works—*The Variation of Animals and Plants under Domestication*, *The Descent of Man and Selection in Relation to Sex*, and *The Expression of the Emotions in Man and Animals*—and two minor (though still important) ones; and if we take the period of 22 years we have to add five more volumes, ending with his last book, the fascinating study of earthworms.[17]

The emergence of Darwinism, I would say, covered the 14-year period from 1858 to 1872; and it was in full flower until the 1890's, when Bateson initiated the anti-Darwinian reaction. This in turn lasted for about a quarter of a century, to be succeeded by the present phase of Neo-Darwinism, in which the central Darwinian concept of natural selection has been successfully related to the facts and principles of modern genetics, ecology and palæontology.

When we biologists take stock of our subject to-day, we speedily discover the magnitude of Darwin's contribution; we see how much of his thought has become incorporated in the permanent framework of our science, how many of his ideas are still alive and fruitful. In the first place, we build on his demonstration that evolution has taken place, and has taken place by natural means, so that both its course and its mechanism can be further investigated by scientific methods. Then his ideas of continuity and gradual transformation remain basic for evolutionary biology—abrupt changes of large extent, as in polyploidy, are exceptional. He stressed the importance of time as a factor in evolution: for selection to produce changes of large extent, time must be forthcoming in enormous quantities—how enormous, we have only recently realized. It is by following out such ideas that evolutionary biologists are now calculating the actual rates of evolution in different groups.

The principle of natural selection was Darwin's greatest discovery, and it remains central to all biological thinking. Darwin's tenacious and comprehensive mind insisted on deducing all possible general conclusions from the principle and on pursuing its implications to the limit. Thus natural selection, he saw, implied that evolutionary change would be gradual and slow. But perhaps his conclusions on biological improvement afford the most remarkable example of his capacity for bold yet careful generalization. Natural selection, he wrote, has as its 'ultimate result . . . . . that each creature tends to become more and more improved in relation to their conditions. This improvement inevitably leads to the gradual advancement of the organisation of the greater number of living beings throughout the world.'[18]

The first sentence refers to small-scale processes, and makes intelligible the omnipresence of detailed adaptation, or biological fitness as some modern workers prefer to call it. It also implies the point made explicitly by Darwin elsewhere[19], that natural selection can never produce characters which are solely or primarily useful to another species. The second sentence, referring to long-term evolution, extends the idea of improvement to cover improvement in general organization, and seems to be the first scientifically based argument for the inevitability of biological progress or evolutionary advance.

He saw the implications of intra-sexual competitive selection in producing masculine weapons, and of inter-sexual allæsthetic selection in generating masculine adorn-

[17] This was the expansion of a paper published 43 years previously.

[18] *Origin*, ch. 4, p. 127.

[19] *Origin*, ch. 4, p. 87.

ments and displays.[20] In *The Expression of the Emotions* he laid the foundations for the modern science of comparative ethology. The very title of the book illustrates his robust naturalism: he saw clearly that the mental and physical characters of organisms are inseparable, and that emotions and intelligence must evolve as much as brains and bodily organization. He did not hesitate to extend his argument to cover man's distinctive mental capacities, intellectual, æsthetic, and moral.[21] While subscribing to the view that 'the moral sense or conscience constitutes by far the most important differences between man and lower animals', he considered that it had evolved naturally.[22] I cannot forbear from quoting one characteristic passage: 'The following proposition seems to me in a high degree probable—namely that any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well, or nearly as well developed, as in man'—though, he adds, it might not be identical with ours. And later he states that 'the belief in spiritual agencies naturally follows from other mental powers.'[23]

It is clear that Darwin had fully grasped the important point that certain characters are what may be called consequential, arising in evolution as a consequence of the prior appearance of some other character, or because correlated with a change brought about by natural selection. Elsewhere Darwin stated this conclusion in general terms—'Owing to the Laws of Correlation, when one part varies or the variations are accumulated through natural selection, other variations, often of the most unexpected nature, will ensue.'[24]

Another of Darwin's notable deductive conclusions concerns divergence (or *cladogenesis* as Rensch has called it). He was the first to realize that natural selection will lead inevitably to evolutionary divergence, both the small-scale divergence of related species, and the large-scale divergence which results in the appearance of distinct and well-defined group-units—genera, families, orders—in a hierarchical arrangement. Through the process of divergence each species exploits the resources of the environment more effectively, so that the large-scale result of divergence in the inhabitants of a region is comparable to the physiological division of labour in an individual body.[25]

Darwin was the first to see the evolutionary explanation of the facts, later subsumed by Haeckel under the head of recapitulation, concerning 'the wide difference in many classes between the embryo and the adult animal, and of the close resemblance of the embryos within the same class.'[26]

His studies on cross-fertilization, and the mechanisms for securing it, paved the way for modern work on heterosis or hybrid vigour (and its application in the hybrid corn industry), and for a general theory of breeding systems, such as C. D. Darlington has so successfully propounded. In combination with his exhaustive survey of variation under domestication, they contributed materially to the development of the sciences of plant and animal breeding.

Finally, I must mention his conclusions on the processes by which new and successful types originate. While recognizing the importance of isolation, which we now regard as a necessary pre-requisite for the separation of one species into two[27], he laid greater stress on the numerical abundance of the evolving species and the size of the area occupied by it. Greater abundance gives more chance for favourable variations to occur ; greater size and diversity of area leads to more vigorous competition for survival, as well as providing greater opportunities for temporary isolation. All this will promote more rapid evolution, and the successful types will have a greater capacity for dispersal and for further evolutionary differentiation.[28] In this, Darwin anticipated in a remarkable way modern views on the factors underlying the origin, spread, and diversification of new types, new unit-steps in the evolutionary process.[29]

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[20] See below, p. 9.

[21] *Descent of Man*, 2nd ed., chs. 3–5.

[22] Mrs Darwin was very antipathetic to the idea that all human morality has 'grown up by evolution' (see *Emma Darwin*, by Mrs Lichfield, privately printed edition, 1904, vol. **2**; p. 360) and was anxious to avoid any suspicion that Darwin regarded spiritual beliefs as no 'higher' than their animal origins. She persuaded Francis Darwin to cut out various passages on the subject from the MS. of the Autobiography which his father had left for posthumous publication (see Nora Barlow, *passim* where the excised passages have been restored).

[23] *Descent of Man*, 2nd ed., ch. 4, p. 149; p. 194.

[24] *Origin*, ch. 4, p. 86: see also ch. 1, p. 11: and p. 207.

[25] *Origin*, ch. 4, p. 116.

[26] *Autobiography*, L. and L., **1**; 86.

It is also, I think, of interest to examine some of Darwin's errors and omissions in the light of our present knowledge. His theory of sexual selection has been the target for bitter and sometimes violent attack. It is true that he did lump together various kinds of display, notably hostile display against rivals and sexual display to potential mates ; and that he ascribed much too great importance to female choice. But he grasped the essential point, that striking displays must have a biological significance, and must be what we now call *allæsthetic* in character, exerting their effect by stimulating the emotions of another individual *via* its visual or auditory senses. And he was quite correct in ascribing the evolution of masculine weapons to intra-sexual selection as between competing males.

Strangely enough, though he mentions cases where adornments are equally developed in both sexes, he dismissed the possibility of biologically effective mutual display between the actual or potential mates. Yet such displays are frequent and often striking, and must have been seen by naturalists before Darwin wrote the *Descent of Man*.[30] I suspect that he was too deeply committed in his thinking to the ideas of female choice and male competition to envisage the possibility of mutual allæsthetic stimulation. Further, in his treatment of the subject he states that sexual selection 'acts in a less rigorous manner than natural selection', because 'the latter produces its effects by the life or death at all ages of the more or less successful competitor', while with the former, the less successful males merely 'leave fewer, less vigorous or no offspring.'[31]

This strange error springs, I would guess, from his failure—perhaps inevitable at the time—to think quantitatively on the subject, coupled with his adoption of the phrase *the struggle for existence*, with its implications of an all-or-nothing competition, life or death. If he had ever spelled out natural selection in modern terms, as being the result of the differential reproduction of variants, he would at once have seen that any form of selection can vary in rigour according to circumstances, and indeed that intra-sexual selection between males in a polygamous species is likely to attain maximum selective intensity.

Strangely enough, elsewhere Darwin drops his all-or-nothing view and assumes a differential action of natural selection. This is, so far as I know, the one major point which he failed to think out fully and on which he expressed divergent conclusions.

Though Darwin, like T. H. Huxley, thought very little of Lamarck's views on the mechanism of evolution—in a letter of 1844 to Hooker he writes 'Heaven defend me from Lamarck nonsense of a "tendency to progression", "adaptation from the slow willing of animals, etc".'[32]—he did believe in the inheritance of certain 'acquired characters'—the effects of the conditions of life and of use and disuse. Furthermore, he attached more importance to them in later editions of the *Origin*. It is this error, which for want of a better term we may loosely call Lamarckian, with which present-day biologists most often reproach Darwin.

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[27] See e.g. Mayr, E., *Systematics and the Origin of Species*, New York, 1942.

[28] *Origin*, ch. 4, p. 107.

[29] See P. J. Darlington, *Zoogeography*, New York and London, 1958 ; also E. Mayr.

[30] It is, however, a curious fact that no such displays seem to have been scientifically described until much later.

[31] *Descent of Man*, 2nd ed. p. 349 ; see also *Origin*, ch. 4, p. 89.

[32] L. and L., **2** ; 23. See also **2** ; 29, 39, 207, 215 ; **3**, 14, 15 : and for Huxley's views, **2** ; 189. Darwin came to adopt a similar attitude to the evolutionary views of his grandfather Erasmus Darwin, expressed in his *Zoonomia*, as being mainly mere speculation, insufficiently supported by facts.

It must be stressed, however, that he regarded these agencies as quite subsidiary to natural selection, which he consistently maintained was much the most important agency of evolutionary change.

These 'Lamarckian' errors clearly sprang from the total ignorance of 19th century biology on the subject of heredity. Fleeming Jenkin pointed out in 1867 that, on the current theory of blending inheritance, even favourable new variations would tend to be swamped out of effective existence by crossing, if heritable variation in general was rare and infrequent.[33] It was to provide for sources of more abundant variation that Darwin came to ascribe increased importance to the evolutionary role of 'acquired characters'. Only when the actual genetic mechanism had been discovered and its particulate (non-blending) nature had been established, could it be shown—notably by R. A. Fisher—that Lamarckian (and orthogenetic) theories of evolution were not only unnecessary but inherently incorrect.

Disuse often does result in evolutionary degeneration: but, as H. J. Muller has shown, this is the result of mutation and selection, not of the direct inheritance of its somatic effects.

Changed conditions again may have evolutionary results—but again not through their direct effects. They may result in increased variability, as Darwin stressed. But this is merely due to rare mutants and new combinations being able to survive in the altered conditions, and also to their arising as a result of inbreeding.

In other cases a character which looks like a modification, a direct response to environmental conditions, turns out to be hereditary. We now know that such apparently Lamarckian results may be obtained in a non-Lamarckian way, by what Waddington calls *genetic assimilation*.[34] With characters which in normal stock are only produced by special environmental stimuli (for instance, reduced cross-veins in Drosophila wings by high temperatures), selection of those individuals showing the character in extreme form may, in a comparatively few generations, lead to the character appearing in a few individuals without exposure to the special stimulus; and further selection, in normal environmental conditions, will produce an overwhelming majority showing the character.

The developmental process leading to the phenotypic manifestation of such a character has both environmental and genetic determinants. During assimilation the genetic determinant has been strengthened, by selection for genes favouring manifestation, to a point at which the process has been genetically canalized and the environmental determinant is no longer required. But since selection acts not on genotypes but on phenotypes, the environmental determinant was originally necessary to produce something on which selection could operate. The result is a modernized version of Baldwin and Lloyd Morgan's organic selection. Thus assimilation, not the inheritance of acquired characters in the usual sense, could account for the origin of various adaptations, such as genetically determined callosities in the exact situations where they are specially required, and many adaptive features of plant ecotypes.

Other adaptations, however, such as those of the hard parts of holometabolous insects, or those involving mimetic resemblance, demand explanation (as Darwin fully realized) in terms of natural selection acting on adaptively random genetic variation. But when virtually nothing was known about the mechanism of reproduction, heredity, and development, many phenomena were more readily interpreted on a non-selectionist basis.

It has been suggested that Darwin would have avoided falling into these pitfalls if only he had paid attention to Mendel's work, which was published in 1865, in plenty of time for Darwin to amend his views in later editions of the *Origin*. I do not think this is so. It needed nearly 20 years of intensive research on suitable material such as *Drosophila* before the findings of genetics could be fruitfully integrated with evolutionary theory. Before that, most geneticists, obsessed by the obvious mutations with large effects which they naturally first studied were led to anti-selectionist views and to the idea that evolution would normally take place by discontinuous steps, or even merely as the result of mutation-pressure. Only when they had arrived at a true picture of the genetic constitution as a flexible gene-complex in which many genes of small effect collaborate to produce phenotypic characters, only then could they see that discontinuity in the genetic basis of variation need not imply discontinuity in its phenotypic manifestation. Consequently evolutionary change, though due to selection of genetically discontinuous variants, can normally be continuous.

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[33] L. and L., 3; 167.

[34] See Waddington, C. H. *The Strategy of the Genes*, Allen and Unwin, 1957.

Darwin had already arrived at this correct conclusion without any knowledge of the underlying mechanisms involved. With his usual common-sense he concentrated on phenotypes; accordingly, continuous variation and gradual change became essential in his thought. I suspect that if he had known of Mendel's results he would have regarded them as interesting but exceptional and relatively unimportant for evolution, as he had already done for other cases of large mutations and sharp segregation. A premature attempt at generalizing Mendelian principles would merely have weakened the central Darwinian principle of gradual slow change.

There is, finally, Darwin's failure to recognize explicitly the radical differences between man and other animals, especially between the process of evolution in man and in other animals. It is true that he speaks of high intellectual power and conscious morality as distinctive attributes of our species, and implies that human speech is something *sui generis* as a means of communication[35]; it is true that he regards man as the highest product of evolution.[36] But nowhere does he point out man's truly unique and most important characteristic—cumulative tradition, the capacity for transmitting experience and the fruits of experience from one generation to the next; nor does he discuss the implications of this new human mechanism of change, as he did so exhaustively for the biological mechanism of natural selection. Thus, while overwhelmed by the thought that modern Europeans must be descended from ignorant savages, like the naked Fuegians who burst on his astonished sight, he makes no attempt to discuss or even to point out the fact that evolution from the savage to the civilized state involves essentially not a biological but a cultural change.

Why was this? I suggest that it was because Darwin's primary and main aim was to provide convincing evidence that organisms were not immutable creations but had evolved by natural means from something different; and this implied a focussing of attention on their past history. This preoccupation of his with origins is revealed in the titles he chose for his two greatest works—*The Origin of Species* and *The Descent of Man*—though *The Evolution of Organisms* and *The Ascent of Man* would in fact have been more appropriate.

His tactics were probably sound: at the time, the main need was to establish on a firm basis the *fact* of evolution and its scientific comprehensibility. In recent years, however, we have turned our attention to the *course* of evolution; and as a result, have been enabled to reach a number of important conclusions about the evolutionary process in general, and our own place and role within it in particular. This has been largely thanks to the soundness of the foundations, both of fact and of idea, provided by Darwin.

That evolution is a natural process, involving man as well as all other organisms in its unbroken continuity: that natural selection inevitably generates novelty, adaptive improvement, and advance in general organization: that successful types tend to differentiate into dominant groups : that improvement of the mental capacities of life, or as I would prefer to put it, advance in the organization of awareness, has been one of the most striking trends in the evolution of higher animals, and has led naturally to the appearance of the distinctive mental and moral qualities of man—these ideas of Darwin, I would say, have been especially important for the later development of evolutionary theory.

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[35] *Descent of Man*, 2nd ed., p. 932.

[36] *Ibid.*, pp. 946–947.

The study of evolution's course, following up Darwin's ideas on divergence and the formation of dominant groups, has revealed that evolutionary advance occurs in a series of steps, through a succession of dominant types. This is the result of very long-term selection, selection between types or groups instead of between individuals. The more efficient type will automatically tend to spread and differentiate at the expense of the less efficient : it is as simple as that. As a result, the more efficient type evolves into a large and successful group, while earlier groups with which it competes are reduced. Taxonomic groups are thus organizational grades as well as phylogenetic units. And the grade is the unit of evolutionary advance. On the large and long-term scale this process results in the familiar but essential fact of the succession and replacement of large dominant groups, each embodying some important new improvement and constituting a new organizational grade.

Sooner or later, each group realizes all its inherent possibilities and becomes stabilized, incapable of major advance except through the rare event of some line evolving an organization with new advantages, and so permitting a break-through to a new grade of advance. This, it seems, can never happen twice, for competition with the established successful type will automatically prevent a second invasion of the same evolutionary territory.

This was an important clarification of the biological scene. Meanwhile, the window that Darwin opened into the world of life permitted a new and evolutionary view of other subjects. Men began studying the evolution of nebulae and stars, of languages and tools, of chemical elements, of social organisations. Eventually they were driven to view the universe at large *sub specie evolutionis*, and so to generalize the evolutionary concept in fullest measure. This extension of Darwin's central idea—of evolution by natural means—is giving us a new vision of the cosmos and of our human destiny.

Evolution in the most general terms is a natural process of irreversible change, which generates novelty, variety, and increase of organization : and all reality can be regarded in one aspect as evolution. Biological evolution is only one sector or phase of this total process. There is also the inorganic sector and the psycho-social or human sector. The phases succeed each other in time, the later being based on and evolving out of the earlier. The inorganic phase is pre-biological, the human is post-biological. Each sector or phase has its own characteristic method of operation, proceeds at its own tempo, possesses its own possibilities and limitations, and produces its own characteristic results, though the later phases incorporate some of the methods and results of the earlier ones.

The inorganic phase operates by physico-chemical interaction, proceeds with extreme slowness, and produces only low degrees of organization. On our earth and probably on a number of other planets, conditions favoured the production of more complex chemical compounds, culminating in substances capable of self-reproduction and self-variation, and therefore subject to a new mechanism of change—natural selection. The passing of this critical point initiated the organic phase of evolution, which proceeded at a much quicker tempo, produced far more variety, and reached far higher levels of organization. The great novelty of the biological phase was the emergence of awareness—psychological or mental capacities—to a position of increasing biological importance.

Eventually, in the line leading to man, the organization of awareness reached a level at which experience could be not only stored in the individual but transmitted cumulatively to later generations. This second critical point initiated the human or psycho-social phase of evolution. In this phase, though natural selection and physico-chemical interaction continued to operate, they were subsidiary to the new mechanism of change based on cumulative cultural tradition. As a result its tempo was again much accelerated, it reached still higher levels of organization, and it produced quite novel results, such as laws, philosophies, machines, and works of art.

In broadest terms, the biological phase of evolution stems from the new invention of self-reproducing matter, the human phase from that of self-reproducing mind.

Man's acquisition of a second mechanism, over and above that of the chromosomes and genes, for securing both evolutionary continuity and evolutionary change, a mechanism based on his capacity for conceptual thought and symbolic language, enabled him to cross the barrier set by biological limitations and enter the virgin fields of psycho-social existence. By the same token he became the latest dominant type of life, shutting the door on the possibility of any other animal making the same advance and disputing his own unique position.

In the light of these facts and ideas, man's true destiny emerges in a startling new form. It is to be the chief agent for the future of evolution on this planet. Only in and through man can any further major advance be achieved—though equally he may inflict damage or distortion on the process, including his own evolving self.

It is in large measure due to Darwin's work on biological evolution that we now possess this new vision of human destiny, and only by using Darwin's naturalistic approach in tackling the problems of psycho-social evolution can we hope to understand that destiny better and to fulfil it more more adequately.

Evolution in the psycho-social phase is primarily cultural: it is predominantly manifested by changes in human cultures, not in human bodies or human gene-complexes. (I am, of course, using *culture* in its broad anthropological and sociological sense, to include art and language, religion and social organization, as well as material culture.)

But, though it thus differs radically from evolution in the biological phase, the process is still a natural phenomenon, to be studied by the methods of science like other natural phenomena. Machines, works of art, social organizations, educational systems, agricultural methods, religions, yes, and even men's values and ideals, are natural phenomena, at once products of and efficient agencies in the process of cultural evolution. The rise and fall of empires and cultures is a natural phenomenon, just as much as the succession of dominant groups in biological evolution.

Cultural evolution is based on the cumulative transmission of experience and its fruits, which provides a second system of heredity and variation, in addition to the biological system embodied in the gene-complex: for brevity's sake we can call it tradition. Thus the selective mechanism which determines what elements shall be incorporated and what rejected in the system of tradition, and so decides between alternative courses of cultural evolution, must be primarily psychological or mental, involving human awareness instead of human genes, and directed towards the satisfaction of felt needs, instead of merely tending towards the survival of the more biologically fit: further, it operates only within the framework of human societies. We may call it *psycho-social selection.*

Though natural selection is an ordering principle, it operates blindly; it pushes life onwards from behind, and brings about improvement automatically, without conscious purpose or any awareness of an aim. Psycho-social selection too acts as an ordering principle. But it pulls man onwards from in front. For it always involves some awareness of an aim, some element of true purpose. Throughout biological evolution the selective mechanism remained essentially unchanged. But in psycho-social evolution the selective mechanism itself evolves as well as its products. It is a goal-selecting mechanism, and the goals that it selects will change with the picture of the world and of human nature provided by man's increasing knowledge.

Thus as human comprehension, knowledge and understanding increase, the aims of evolving man can become more clearly defined, his purpose more conscious and more embracing.

In the light of our present knowledge man's most comprehensive aim is seen not as mere survival, not as numerical increase, not as increased complexity of organization or increased control over his environment, but as greater fulfilment—the fuller realization of more possibilities by the human species collectively and more of its component members individually.

Darwin ended the *Descent of Man* with this characteristic passage: 'Man may be excused for feeling some pride at having risen, though not through his own exertions, to the very summit of the organic scale; and the fact of his having thus risen, instead of having been aboriginally placed there, may give him hope for a still higher destiny in the distant future. But we are not here concerned with hopes or fears, only with the truth as far as our reason permits us to discover it.'

To-day, building on the foundations provided by Darwinism, we can utilize evolutionary concepts in thinking about the history and future of our species. Human destiny need no longer be merely an affair of hopes and fears. In principle, it can be rationally defined on the basis of scientific knowledge, and rationally pursued by the aid of scientific methods. Once greater fulfilment is recognized as man's ultimate or dominant aim, we shall need a science of human possibilities to help guide the long course of psycho-social evolution that lies ahead.

On this centenary occasion we commemorate not only the birth and emergence of Darwinism, but also its achievement. In the past hundred years it has given us a comprehension of the biological past, and that comprehension is now beginning to illuminate the human future.

ADDENDUM

The following incident only came to my notice after this address was printed. Edmund Gosse, in *Father and Son*, records that already in 1857 the question of man's descent 'from an orangutan' was being heatedly discussed, and that Lyell, anticipating that the announcement of 'the doctrine of natural selection' would provoke a public outcry, felt that a bodyguard of sound and experienced naturalists, expert in the description of species, should be privately made aware of its tenour'. Philip Gosse, F.R.S., was one of these and was accordingly 'spoken to by Hooker, and later by Darwin after meetings of the Royal Society in the Summer of 1857'.

However, instead of being converted, he was provoked into writing that extraordinary work *Omphalos* which attempted to reconcile geology with Genesis by claiming that all things must have been created perfect, in a completely developed state, so that Adam would have had a navel, and the earth would have appeared complete with all the rock-layers and fossils it would have contained if evolution had actually occurred! He must have worked fast, for the book was published during the same year.

Strangely enough, I can find no reference to Philip Gosse in the Life & Letters of Darwin or of Hooker.

These facts indicate that in 1857 Lyell & Hooker must have thought that Darwin would be ready to publish his monumental work on Evolution by natural selection in the near future, whereas I consider that he would almost certainly have dragged it out for a number of years, if it had not been for Wallace.

DARWIN'S VIEWS ON THE RELATIONS BETWEEN EMBRYOLOGY AND EVOLUTION

by Sir Gavin de Beer, F.R.S.
(*Director, British Museum* (*Natural History*).)

Introduction.

It has so long been thought that the relations between embryology and evolution were governed by the theory of recapitulation, that the discrediting of this theory has resulted in an impression that those who reject it also reject any relation between evolution and embryology. This is far from being true. It will be helpful to clear up the point by reference to the use which Darwin himself made of the argument of embryology when building up his case for evolution. Here, as in many other aspects of his work, it will be found that Darwin was nearer to what is now believed to be the truth than were some of his contemporaries. This can be shown by considering the progress of the theory of evolution in Darwin's own mind, as revealed by the *Sketch* of 1842, the *Essay* of 1844, and the successive editions of the *Origin of Species* in which he incorporated some of his contemporaries' views and arguments.

Before embarking on the analysis of Darwin's own views on embryology, it will be necessary to make a few essential preliminary observations. First it must be realized that at the time when Darwin was working, knowledge of embryology was in its infancy and amounted to little more than the foundations laid by von Baer in 1828, and they were purely descriptive. Not only was knowledge of comparative embryology extremely scanty, but the concept of experimental or causal embryology had not yet appeared at all.

Next it must be remembered that scientific understanding of heredity was non-existent before Mendel's work which was published in 1866, but only rescued from oblivion and recognized in 1900. All that Darwin had to go upon was a belief that like tends to beget like, and that the effect of a cross between parents of different characters was a blend. It will be noticed that such a view of heredity must lay stress on the search for resemblances between parents and offspring, for they are the only positive points of comparison, whereas the modern science of genetics is concerned with the distribution of variants among the offspring of parents, and is interested in differences no less than in resemblances between them.

Finally it must be pointed out that in Darwin's time, the study of embryonic development was still hampered by a confusion between two categories of thought representing different branches of science. The succession of stages between the egg and the adult is the proper field of embryology, but it was appealed to in order to provide an explanation of the resemblance between the adult and its parent, or in other words, of heredity. In his theory of pangenesis, Darwin imagined the existence of particles which were supposed to come from the different parts of the body of the parent and to be transmitted through the germ-cells to the offspring, which they then moulded so that it differentiated into a body like that of its parent. The cause of embryonic development and that of hereditary resemblance were thus combined. The result is that in the argument which Darwin derived from embryonic development for evolution, he is sometimes talking embryology and sometimes genetics.

Embryology in the Sketch of 1842.

In the *Sketch* of 1842, embryology is first appealed to for an explanation of the general unity of type which is shown by each group of animals. The appeal is to the similarity between early embryos of fish, birds and mammals, and, within the mammals, to the similarity at early stages of development between the rudiments of the wing of the bat, the hoof of a horse, the paddle of a seal, and the hand of a man. Here, Darwin is following von Baer in the latter's law of embryonic resemblance, and is using it to support his argument that the unity of type shown by animals within a group can only be explained by their common descent, and therefore by their mutual affinity. The argument is morphological and genetic, and embryos are used as additional material on which to demonstrate resemblances. It is incontrovertible.

There follows a passage which shows that already in 1842 Darwin had grasped not only the significance of von Baer's law of progressive differentiation, but had also anticipated Fritz Müller's principle of progressive deviation. It runs as follows: " It is not true that one [form in its development] passes through the form of a lower group, though no doubt fish more nearly related to foetal state. They pass through the same phases, but some, generally called the higher groups, are further metamorphosed."[1] This is a succinct and accurate description of what happens in the innumerable cases where the young stages of developing animals resemble each other more than they resemble their adult stages, and more than the adult stages resemble each other. Darwin's adoption of this view shows that he rejected the transcendental theories of Serres and of Meckel on which Haeckel later based his theory of recapitulation.

Darwin's reference to fish as " more nearly related to foetal state ", means that the fish, representing a lower group, are less " metamorphosed " in their ontogenetic development, and that their adults resemble their embryos more than the adults of the higher groups resemble their embryos. It therefore follows that the mammalian " foetal state " or embryo is " more nearly related ", i.e. more similar, to the fish adult than to the adult of higher vertebrates in its ancestry. It is not difficult to see here the importance which Darwin attached to the visceral pouches of the mammalian embryo, and to the fact that the adult fish has gill-slits.

In the similarity between the courses of the arterial arches in the embryos of different vertebrates, Darwin was struck not only by the closeness of their resemblance, but also by the fact that it was quite unrelated to the conditions of life in which the different embryos lived: " How wonderful that in egg, in water [i.e. fish and amphibia] or air [i.e. reptile and bird], or in womb of mother [i.e. in mammal], artery should run in same course."[2] It is one of the strongest arguments for affinity between those forms and for their community of descent; and as they have undergone modification during their descent, it is evidence for evolution.

The lack of correlation between embryonic structures and environmental conditions is then used by Darwin to develop his argument that selection is exerted on the adult, but little or not on the embryo. The structure of each organism is chiefly adapted to the sustentation of its life when full-grown, when it has to feed itself and propagate. " The structure of a kitten is quite in secondary degree adapted to its habits, whilst fed by its mother's milk and prey. Hence variation in the structure of the full-grown species will *chiefly* determine the preservation of a species now become ill-suited to its habitat, or rather with a better place opened to it in the economy of nature. It would not matter to the full-grown cat whether in its young state it was more or less eminently feline, so that it [can] become so when full-grown."[3]

Larvae, on the other hand, are in a different category from foetuses because of their prolonged exposure to environment: " In larvae, which have long life selection, perhaps, does much—in the pupa not so much."[4]

The argument of the greater exposure of the organism to selection in the adult than in the embryo is doubtless true as regards extrinsic selection, although embryos are not immune; it is used by Darwin in conjunction with two other arguments. The first of these is that evolutionary novelties (Darwin called them " variations ") appear at some stage during development (" most variation depends on early change "), and tend to appear in the offspring at the same stage. Before that stage, therefore, there is little or no " variation ", and this is why the early embryos of different classes look alike. After that stage, " variation " is found, and it is on this that selection works, producing results in the later but not in the younger stages. " Look to a foetus and its [adult] parent, and again after ages [to a] foetus and its [adult] descendant ; the [adult] parent more variable than foetus, which explains all."[5]

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[1] *Evolution by Natural Selection*, Cambridge 1958, p. 78.
[2] *Evolution by Natural Selection*, 1958, p. 78.
[3] *Evolution by Natural Selection*, 1958, p. 78.
[4] *Evolution by Natural Selection*, 1958, p. 79.

It may be noticed that in the foregoing argument, Darwin imagined that evolutionary novelties arise during development in the ancestor and tend to appear at the same stage of development in the descendant, which is the point of view adopted to-day. It is contrary to the elaboration by Haeckel of his theory of recapitulation, which required that novelties which are to affect subsequent evolution must arise in the adult of the ancestor and be repeated, abbreviated, and telescoped into earlier and earlier stages of development in the descendants. The notion that the adult of the ancestor was the only stage at which evolutionary novelties of phylogenetic significance could arise, was in accordance with the Lamarckian view of the importance of use and disuse in the initiation of change, since it is in the adult that use and disuse were supposed to operate and produce their effects.

Darwin's second point is concerned with the delayed effect of "variations". When a tendency to an hereditary disease or other condition such as goitre, gout, baldness in man, or the shape of the horns in cattle, is attributed to a common father, it is necessary to believe that something happened at conception the effects of which lie dormant for a long time until the organism is full-grown.

In practising artificial selection for the production of domestic breeds of animals, man selects for the full-grown type. " The hereditary peculiarities characterizing our domestic races. . . . do not appear with their full characters in very early states ; thus though two breeds of cows have calves different, they are not so different —grey-hound and bull-dog. And this is what is to be expected, for man is indifferent to characters of young animals and hence would select those full-grown animals which possessed the desirable characteristics."[6]

Applying the conclusions derived from a study of artificial selection on domestic animals to the effect of selection in nature, the result is therefore to explain the resemblance between embryos as due to their constancy and lack of variation, which in turn depends on the facts that variation chiefly affects later stages of development and that embryos are not exposed to the effects of selection. Since embryos have the same hereditary endowment as adults, it is just as important to explain why embryos resemble each other as it is to explain why their adults differ.

In all the foregoing argument, Darwin is concerned solely to show that resemblance between embryos is evidence of mutual affinity between stocks that have diverged by modified descent from a progenitor, and to explain their divergence in terms of variation and selection and of the different stages in the life-history of organisms at which these factors operate. It is one of the most powerful arguments in favour of evolution and is incontrovertible. Descendants have diverged from a common ancestor, but little has so far been said about what that ancestor looked like, or what information embryology could supply concerning it.

The characterization of the ancestral form creeps into the argument as a result of the application of the evidence of embryology to the problem of classification. " The natural system being on theory genealogical, we can at once see why foetus, retaining traces of the ancestral form, is of the highest value in classification."[7] This statement with which Darwin closes his section on Embryology in the *Sketch* of 1842, is perfectly acceptable to-day, and it will be noticed that while he claims that the embryo retains " traces of the ancestral form " because it has been least acted upon by variation and selection, he does not claim that it represents the form of the adult ancestor.

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[5] *Evolution by Natural Selection*, 1958, p. 81.

[6] *Evolution by Natural Selection*, 1958, p. 80.

[7] *Evolution by Natural Selection*, 1958, p. 81.

Summing up the argument in the *Sketch* of 1842, it may be said that evolution explains the resemblance between embryos of different species because of their community of descent and mutual affinity ; different forms undergo progressive variation during their development ; selection acts on adults and on larvae and modifies them, whereas the embryo is left unaltered and therefore reflects the " ancestral form "; but species do not pass through the adult stages of their ancestors during their development, and there is no pressing back into earlier stages of development of characters which first appeared at later stages. In other words, Darwin's argument is free from the objections which beset Haeckel's theory of recapitulation, and is unreservedly acceptable to-day.

Embryology in the Essay *of* 1844.

Written only a comparatively short time after the *Sketch* of 1842, it would not be expected that the *Essay* of 1844 would differ greatly from it in its general form and concept. It is of course written out instead of being in the form of notes, and it is expanded in phrases of which some are of importance from the point of view of the present inquiry. For instance : " it has often been asserted that the higher animal in each class passes through the state of a lower animal ; for instance that the mammal amongst the vertebrata passes through the state of a fish : but Müller denies this, and affirms that the young mammal is at no time a fish, as does Owen assert that the embryonic jelly-fish is at no time a polyp, but that mammal and fish, jelly-fish and polyp pass through the same state ; the mammal and jelly-fish being only further developed or changed."[8] There is nothing to be altered in this demonstration to bring it into complete agreement with the modern view expressed in the principle of *deviation*, by which is meant that the early embryonic stages of the descendant represent the early embryonic stages of the ancestor, but that the descendant has undergone a different and more extensive later development than the ancestor.

That this was Darwin's opinion is made even more clear in the subsequent passage : " the similar course of the arteries in the mammal, bird, reptile and fish, must be looked at as a most ancient record of the embryonic structure of the common parent stock of these four great classes "[9]. Since such resemblance is inexplicable on the theory of separate creations, this is the important contribution which embryology makes to evolution ; and the embryo of the descendant represents not the adult of the ancestor but its embryo, which determines its plan of structure in the case of vertebrates (but not in other cases such as that of insects).

Finally, the *Essay* of 1844 expresses with great clarity the fact that " variation of structure takes place at all times of life, though no doubt far less in amount and seldomer in quite mature life ".[10] There is little room here for Haeckel's contention that evolution proceeds by piling new adult stages on to old ones.

Embryology in the Origin of Species.

The treatment of embryology in the various editions of the *Origin of Species* follows the same general outlines as the *Sketch* of 1842 and the *Essay* of 1844, but is of course amplified. Embryology is considered under the heading " Mutual Affinities of Organic Beings ". There is, to start with, the argument from general unity of type which embryos show ; and to the embryos of vertebrates are added the " vermiform larvae " of different insects which resemble each other more closely than do their adults. On the other hand, since larvae are under the influence of selection, " cases

[8] *Evolution by Natural Selection*, 1958, p. 224.
[9] *Evolution by Natural Selection*, 1958, p. 230.
[10] *Evolution by Natural Selection*, 1958, p. 229.

could be given of the larvae of two species, or of two groups of species, differing quite as much, or even more, from each other than do their adult parents."[11] In most cases, however, the law of embryonic resemblance holds good, and the similarity between the larvae of cirripedes and those of other Crustacea enabled Vaughan Thompson to show that the cirripedes are Crustacea.

Darwin then goes on to refer to the fact that while some animals show a large amount of change of shape during their development (" metamorphosis ") which may be progressive or regressive, others such as cephalopods and spiders show very little, where " the embryo does not at any period differ widely from the adult ". He then puts the facts in the form of five questions to which answers are required :

1. The difference in structure generally found between an embryo and the adult into which it will develop ;
2. the progressive difference in structure found between different parts of an embryo during development, which parts at the start were alike ;
3. the common (but not invariable) resemblance between embryos or larvae of widely different species in the same class ;
4. the absence of close relation between the structure of the embryo and its conditions of existence, as distinct from larvae living an active life which show marked adaptations to their surroundings :
5. the possibility that the embryo may have a higher degree of organization than the adult form.

Before giving Darwin's answers to these questions, it may be pointed out that the first is aimed at nothing less than the fact of embryonic development itself, too often taken for granted, but appealed to by Darwin as an argument to show that great modification of structure takes place during development from the egg. In later editions of the *Origin of Species* this point is amplified with reference to the production of medusae by polyps, and to alternations of generations. He is out to show that like does not always beget perfect like.

The second question again is embryological, but it had to wait until the application of experimental techniques to embryology before adequate answers could be given to the problem of differentiation. The third question is concerned with the mutual affinity between descendants of a common ancestor ; the fourth relates to the susceptibility of an animal to the effects of selection at different stages of its life ; and the fifth is aimed at the phenomenon of retrogressive metamorphosis and degeneration.

Darwin's explanation of all five questions is based on evolution and on the following two principles :

(*a*) The appearance of modifications at some (not very early) stage during the development,

(*b*) the re-appearance in the offspring of such modifications at stages corresponding to those at which they first appeared in the parent.[12]

To-day these two principles are at the centre of the problem of the time of phenotypic appearance of mutations, of genetics, and of developmental physiology. It was no small achievement on Darwin's part to disengage these principles a century before they became accessible to experimental study.

Darwin shows that these two principles are applicable to man and to domestic animals, where they account for the fact that it is difficult to tell whether a child will grow into a tall or a short adult, that the merit of horses, cattle, and " various fancy animals " cannot be discerned until some time after they have been born, that the characters of the horns in horned cattle only affect the adult, and that the characters of the caterpillar of the silkworm only affect the caterpillar.

Having found these principles useful in explaining certain facts in domestic animals, Darwin next proceeds to apply them to animals in the state of nature. He shows how the appearance of evolutionary novelties in the development of vertebrates may be imagined as having modified the fore limb into wings, paddles or hands, the embryos remaining similar to each other and considerably different from the adults into which they will develop. As already explained in connexion with the *Sketch* of 1842 and the *Essay* of 1844, this is an application of von Baer's laws of embryonic resemblance and progressive differentiation, and of Fritz Müller's principle of progressive deviation. It represents a morphological mode of evolution to which the term *deviation* is now applied.

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[11] *On the Origin of Species*, Ed. 1, 1859, p. 440.
[12] *Origin of Species*, Ed. 1, 1859, p. 444.

In some cases, however, such as cephalopods and spiders, and the short-face tumbler pigeon, the young closely resembles the parent. This is ascribed by Darwin to the appearance of modifications during early stages of development, either because they originally appeared at such stages in the parent, or because they have been inherited by the descendants to appear at an earlier stage than that at which they appeared in the parent. As to the question why such animals during their development should not undergo " metamorphosis " (by which Darwin means marked change). he argues that it could be answered if the young had to provide for its own wants at an early stage of development, and if the habits of life of the young were precisely the same as those of the adult. In other words, selection might cause the young to resemble their parents. On the other hand, in cases where " it profited the young to follow habits of life in any degree different from those of the parent ", such young " might easily be rendered by natural selection different to any conceivable extent from their parents."[13]

The ability of the embryo to represent the ancestral type is given greater weight in the *Origin of Species* than in the *Sketch* of 1842 or the *Essay* of 1844. Since evolution has mostly affected adults, " the embryo is the animal in its less modified state ; and, in so far, it reveals the structure of its progenitor."[14] It is likely that in formulating these sentences, Darwin was influenced by Agassiz's theory of three-fold-parallelism between palaeontological succession, systematic rank, and embryonic development, as is apparent in the following passage :

" As the embryonic state of each species and group of species partially shows us the structure of their less modified ancient progenitors, we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants—our existing species. Agassiz believes this to be a law of nature."[15] It will be noticed that Darwin has not yet said that the embryo of the descendant represents the *adult* state of the ancestor, although this is clearly the implication which Darwin had in mind. But the most important point to notice is the immediate sequel in Darwin's work : " but I am bound to confess that I only hope to see the law hereafter proved true. It can be proved true in those cases alone in which the ancient state, now supposed to be represented in many embryos, has not been obliterated, either by the successive variations in a long course of modification having supervened at a very early age, or by the variations having been inherited at an earlier period than that at which they first appeared."[16]

From this passage it is clear that Darwin did not wish to commit himself too deeply or specifically to the view that the embryo represents the adult ancestor, and this is further shown by the insertion in the 4th edition (1866) of a passage in which the embryo is referred to as " a picture, more or less obscured, of the progenitor, either in its adult or larval state ",[17] which is substituted for " common parent-form of each great class of animals."[18] Further, the reference to the conditions under which an embryo might be expected to reveal ancestral structure, shows that Darwin had appreciated the possibility of evolutionary novelties (which might conceal the ancestral structure) having made their appearance at a very early stage of development, and of their affecting those early stages and sometimes also all the remainder of development, up to and including the adult. These possibilities correspond to the morphological modes now known as *caenogenesis* and *paedomorphosis*.

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[13] *Origin of Species*, Ed. 1, 1859, p. 448.
[14] *Origin of Species*, Ed. 1, 1859, p. 449.
[15] *Origin of Species*, Ed. 1, 1859, p. 449.
[16] *Origin of Species*, Ed. 1, 1859, pp. 449–450.
[17] *Origin of Species*, Ed. 4, 1866, p. 533.
[18] *Origin of Species*, Ed. 1, 1859, p. 450.

It is now believed, that (except where caenogenesis has intervened) the ontogeny of the descendant *repeats* the early stages of the ontogeny of the ancestor, stage for stage, and that it substitutes new and different later stages for the old later stages of the ontogeny of the ancestor. This is only another way of saying that during its development a descendant does not pass through or *recapitulate* stages corresponding to the succession of adult stages of its ancestor, but deviates progressively away from them.

However, in so far as the early stages of development may lay down the general plan of structure of the organism, when a descendant repeats the early stages of the ancestor's ontogenetic development in the early stages of its own development, they may also, though not always, repeat the ancestral plan of structure. This is the basis for the general unity of type of related organisms such as the vertebrates, explicable only by their community of descent, but it supplies no *direct* information on the structure of the adult stage of the ancestor, beyond the *inference* that as the ancestor was *ex hypothesi* more primitive than the descendant, the adult ancestor probably differed less from its young stages than the adult of the descendant differs from its young stages. On the other hand, in the case of insects Darwin realized clearly (see below) that the larva represents no ancestral plan of structure at all.

This definition of the modern position would not have been unacceptable to Darwin at the time when he wrote the *Sketch* of 1842, and the *Essay* of 1844, and even in the *Origin of Species* this point of view is still recognizable in the words: "The embryo is the animal in its less modified state; and in so far, it reveals the structure of its progenitor."[19] Unfortunately, Darwin then went on to adopt Agassiz's view and to say that extinct forms of life resemble the embryos of their descendants.

Here Darwin was flatly contradicted by his champion T. H. Huxley who pointed out as early as 1862 that "there is no real parallel between the successive forms assumed in the development of the life of the individual at present, and those which have appeared at different epochs in the past."[20]

A friend, from some of whose views Darwin might have been saved, was Fritz Müller, for in the 4th (1866) and subsequent editions of the *Origin of Species*, Darwin quoted Müller's view that as the nauplius larva is widespread throughout the Crustacea, "it is probable that at some very remote period an independent adult animal, resembling the Nauplius, existed, and subsequently produced, along several divergent lines of descent, the above-named great Crustacean groups".[21]

Here it is necessary to disagree with the Master. Crustacea are animals whose bodies are subdivided into large and varying number of segments. They were evolved from organisms like trilobites whose number of body-segments was even greater, and, more distantly, from worm-like forms in which the segments were more numerous still. The nauplius, on the other hand, has a very small number of segments and only three pairs of appendages. It represents nothing but the anterior tip of the organism, behind which the remainder later develops. It cannot possibly represent any adult ancestor at all, and is a larval form precociously developed and adapted to a free-swimming mode of life, in which it is capable of carrying out the function of dispersal. Except for the first three pairs of limbs, it does not even lay down a plan of structure for its adults.

The nauplius is evidence for the affinity between the many and various groups of

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[19] *Origin of Species*, Ed. 1, 1859, p. 449; *cf.* Ed. 4, 1866, p. 532; Ed. 6, 1872, p. 396; World's Classics ed., p. 517.

[20] T. H. Huxley: *Scientific Memoirs*, **1**, 303, London, 1898.

[21] *Origin of Species*, Ed. 4, 1866, p. 531; Ed. 6, 1872, p. 395; World's Classics ed., p. 516.

Crustacea which pass through this stage in their life-histories, and have inherited this larval form from a common ancestor which possessed it. The nauplius is therefore evidence in favour of evolution, and this evidence would not be any stronger if the ancestral stage which the nauplius represents were the adult.

Darwin's appeal to embryology for evidence in favour of evolution is in no way affected by the dropping of these additions which he made to the later editions of his book. It may therefore be said that the abandonment of Haeckel's theory of recapitulation in no way reduces the importance of the bearing of embryology on evolution. On the contrary, after the abandonment of the theory of recapitulation, the realization that evolutionary novelties may arise in the young stages of the ancestor and may be delayed into the adult stage of the descendant, has opened up wide new fields of study and explained many problems of evolution.

The application of these new principles which are summed up in the term *paedomorphosis* have been described in works by W. Garstang and A. C. Hardy, N. J. Berrill and myself. Paedomorphosis is the term given to evolutionary results produced by the appearance of novelties in the young stages of the ancestor according to the morphological modes now known as deviation and neoteny. In the former, new stages of development are substituted for old, producing divergence ; in the latter, young stages of development of the ancestor are retarded into the adult stage of the descendant whose previous adult stages have been discarded.

Here it is only necessary to point out that Darwin himself was not far from grasping the principle of paedomorphosis. In the 4th and subsequent editions of the *Origin of Species*, he agreed that " the various larval and pupal stages of insects have thus been acquired through adaptation, and not through inheritance from some ancient form."[22] The use of the argument shows that Darwin recognized the principle of *caenogenesis* or the possibility of appearance of evolutionary novelties in young stages of development. Indeed, he said so explicitly in the following passage: " in a state of nature natural selection will be enabled to act on and modify organic beings at any age, by the accumulation of variations profitable at that age, and by their inheritance at a corresponding age."[23]

That he recognized the importance of this principle for evolution is clear from the passage in which he said: " we can see how by changes of structure in the young, . . . animals might come to pass through stages of development, perfectly distinct from the primordial condition of their adult progenitors "[24]. This corresponds to the mode of evolution now defined as *deviation*. Then Darwin refers to the remarkable caenogenetic adaptation of the parasitic beetle *Sitaris*, and goes on to say : " Now, if an insect undergoing transformations like those of the *Sitaris*, were to become the progenitor of a whole new class of insects, the course of development of the new class would be widely different from that of our existing insects ; and the first larval stage certainly would not represent the former condition of any adult and ancient form "[25]

In this remarkable passage Darwin imagines the possibility of a caenogenetic evolutionary novelty affecting its descendants and giving rise to an entire new Class. He does not specifically state that the adult stages of this new Class will be affected by the caenogenetic evolutionary novelty, but it is implicit in the premiss, since the descendants would not otherwise constitute " a whole new class of insects ". Darwin came therefore near to recognizing that the adult stage of the descendant may reflect the young stages of the ancestor. This mode of evolution, the precise reverse of recapitulation, is now defined as *neoteny*, which has played a most important part in paedomorphosis and is considered to have characterized the evolution of chordates, insects, appendicularians, Cladocera, copepods, siphonophores, ctenophores, ratites, and man, from their respective ancestors.

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[22] *Origin of Species*, Ed. 6, 1872, p. 394 ; World's Classics ed., p. 515 ; it may be compared with the corresponding passage in *Origin* Ed. 4, 1886, p. 530.

[23] *Origin of Species*, Ed. 6, 1872, p. 67 ; World's Classics ed., p. 87.

[24] *Origin of Species*, Ed. 6, 1872, p. 394 ; World's Classics ed., p. 515.

[25] *Origin of Species*, Ed. 4, 1866, p. 531 ; Ed. 6, 1872, p. 395 ; World's Classics ed., p. 516.

It may also be noticed that Darwin acknowledged the possibility of variation in time of appearance of a structure in the life-history of ancestors and descendants and the importance of this principle for the solution of evolutionary problems. His example was a simple one, but the principle is clearly defined. Called upon to explain the parthenogenesis found in the *larva* of Cecidomyidae, he pointed out that it also occurred in the *pupa* of Chironomidae and in the *adult* female of Coccidae: "We have only to accelerate parthenogenetic reproduction by gradual steps to an earlier and earlier age, . . . and we can perhaps account for the marvellous case of the Cecidomyia."[26] This is the principle known to-day as *heterochrony*.

When Darwin wrote the *Origin of Species*, several years were still to elapse before the experimental method was introduced into embryological research, and before the establishment of *Entwicklungsmechanik* as a recognized branch of science accustomed biologists to think of ontogenetic development in terms of cause and effect, stimulus and response. In those early days embryological work was purely descriptive, and yet, here again, Darwin showed the measure of his insight when he deliberately considered "at what period of life each variation may have been caused", and "at what period the effects are displayed".

This is not the first occasion on which an attempt has been made to appraise Darwin's views on embryology. It was done fifty years ago by Sedgwick in an article of remarkable force in which, while extending full credit to Darwin for the impetus which his work gave to embryological studies, he showed how inadequate and fallacious Haeckel's theory of recapitulation was, for which reason he criticized this aspect of Darwin's work. It would almost seem as though the value of Darwin's speculations on the significance of embryological development is now more highly appreciated than it was.

When it is remembered how limited was the state of knowledge of embryology when Darwin wrote, it is wonderful to see how sound was his judgment, both in argument and in imagination, when describing the relations between embryology and evolution.

Note: "Evolution by Natural Selection" 1958 is published by the Cambridge University Press for the XVth International Congress of Zoology and the Linnean Society of London, and contains Darwin's "Sketch of 1842" and his "Essay of 1844."

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[26] *Origin of Species*, Ed. 6, 1872, p. 387; World's Classics ed., p. 506.

PATTERNS OF COLONIAL DEVELOPMENT IN GRAPTOLITES

By O. M. B. Bulman, F.R.S.

(*Woodwardian Professor of Geology, the University, Cambridge.*)

(With 7 text-figures.)

Graptolites are extinct colonial organisms of which the zooids were housed in linear series of chitinous thecae arranged uniserially along the branches of a ramifying rhabdosome, or uniserially or biserially along a single branch. The nature of the organisms is doubtful, but certain structural features of the skeleton, such as the presence of a stolon-system and the histology of the periderm, suggest closer affinities with the Stomochorda than with any other living group. The rhabdosome often exhibits great regularity in branching and in many genera a steady and progressive change in thecal form. It is difficult to make completely objective generalizations, and our knowledge of structural details still covers a relatively small part of the whole field, but some aspects of the rhabdosome patterns formed are discussed below.

Thecal Budding

The true graptolites or Graptoloidea are with reasonable confidence derived from the dendroid graptolites or Dendroidea through a transitional family (the Tremadocian Anisograptidae) assigned to the Dendroidea because of its typically dendroid branch structure. This structure is more complicated than that of the Graptoloidea and consists of three types of theca produced in regularly alternating triads related to a fully chitinized stolon-system. Of these three types, the autothecae and bithecae appear to have been occupied by dimorphic zooids, while the stolothecae had seemingly no distinct type of zooid, but are rather the immature proximal portions of successive autothecae (Fig. 1A, B). Growth-lines of each stolotheca pass uninterruptedly into those of the succeeding autotheca, but the bithecal and daughter stolothecal growth-lines are " unconformable ". It is thus to be inferred that each autothecal zooid has been in turn the terminal zooid of the branch.

Along the branches of the Graptoloidea, only one type of theca is present, and of this the metathecal portion seems to correspond to the autotheca of the dendroid, with a prothecal portion (Fig. 1C, D) corresponding to the dendroid stolotheca. If any actual stolons were present, they must have been unchitinized. Growth-line evidence again reveals a sympodial method of growth of the stipe. It has been conjectured (Kozlowski, 1949) that the dendroid dimorphism was probably sexual, the autotheca corresponding to the female zooid, and that evolution of the epiplanktonic Graptoloidea was accompanied by a transition to hermaphroditism.

Branching Mechanism.

Branching in the Dendroidea is preceded by the production of two stolothecae at a single stolonal node, the extra stolotheca in all known examples replacing the bitheca of a normal triad (Fig. 1E). Since the stolothecae are merely immature autothecae, this means in effect that a branching division results from the formation of two autothecae in place of the normal autotheca and bitheca (or, conjecturally, of two female zooids in place of the male and female pair).

This branching is in many dendroids quite irregular, but the siculate *Dictyonema flabelliforme* (Eichwald) may show an approach to regularity, and regularity of branching is apparent in many of the descendant anisograptids. The branching nodes must have been formed at approximately the same time at most or all growing points of

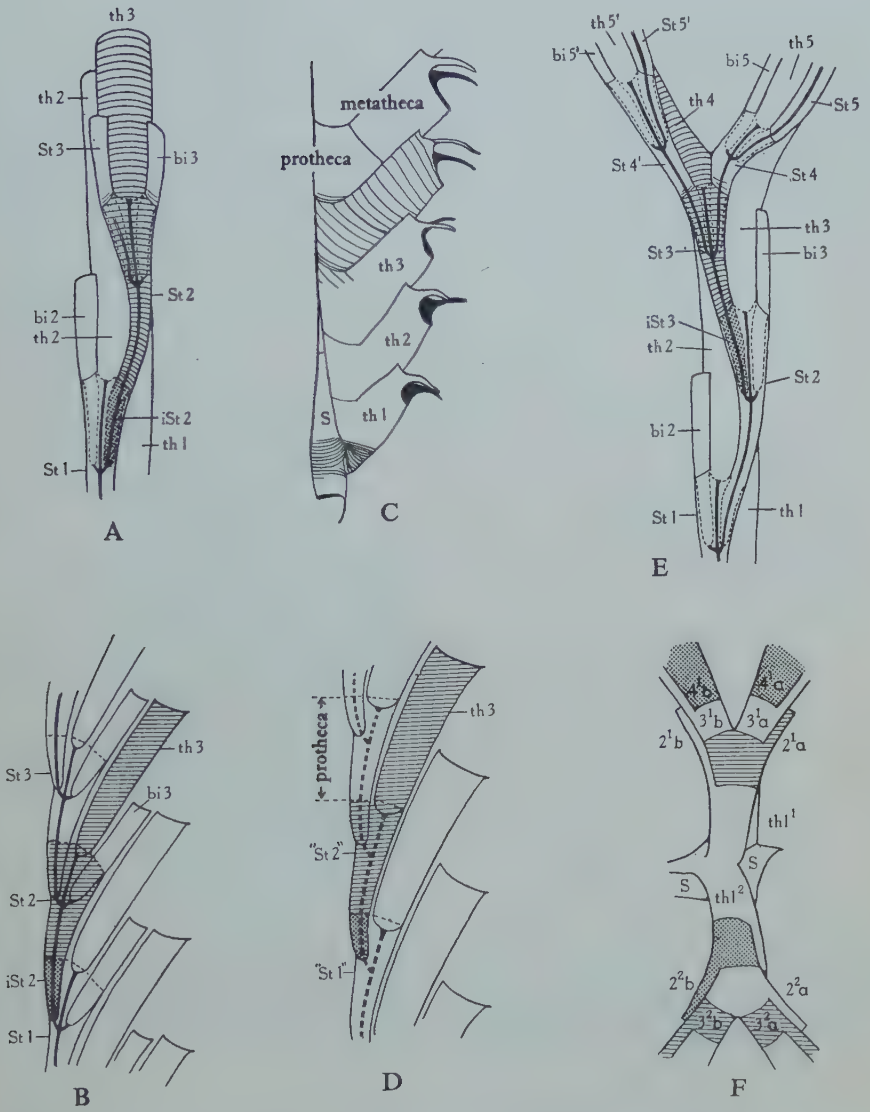

Fig. 1.—Budding and branching mechanisms in the Dendroidea and the Graptoloidea.

A, Diagrammatic figure of distal (growing) end of a dendroid stipe (branch) from the dorsal side, showing relations of the three types of thecae to each other and to the stolon-system ; B, schematic representation of dendroid branch structure. C, Lateral view of proximal end of a graptoloid (*Monograptus chimaera* (Barrande)) showing relations of the protheca and metatheca; D, schematic representation of graptoloid stipe to illustrate relation to dendroid structure. E, Diagrammatic figure of the division of a dendroid stipe with the production of two stolothecae. (*St* 4, *St* 4′). F, Diagrammatic figure of the proximal end of the rhabdosome of *Tetragraptus bigsbyi* (Hall) showing in dorsal view relations of the early thecae and the " double buds " 3^1a, 3^1b and 3^2a, 3^2b.

*St*1, 2 etc., stolothecae ; *iSt*2, 3, internal proximal portions of stolothecae ; *th*1, 2 etc., autothecae ; *bi*1, 2 etc., bithecae ; *s*, sicula. Stolon-systems shown in heavy black lines ; the stolon-system indicated by broken lines in fig. 1D is entirely hypothetical.

the rhabdosome, and the frequency with which they recur is regular, and shows in general a steady decrease during rhabdosome growth. Absolute regularity is rarely if ever attained, and higher " orders " of branching generally tend to be more irregular than the lower ones, but the capacity for branching (the number of " orders " produced in the adult) and the frequency (which determines the length of successive " orders " of branch) are specific characters of most anisograptids and a part of the genetic " make-up " of the species. A few of the very large number of *Clonograptus* species, shown in Fig. 2, will serve to illustrate this. *Anisograptus* furnishes an example of a slightly different sort ; in *A. matanensis* (Fig. 3B), (and *A. norvegicus*) one of the three primary stipes divides at slightly more than 1 mm. length (probably after the formation of one theca) while the other two attain a length of 4–5 mm. before the first dichotomy, and exceptions to this are so rare as to be considered abnormalities, whereas in *A. richardsoni* (Fig. 3C) (and *A. grandis*) all three primary stipes are of comparable length. The regularity of first-order branching in *A. matanensis* does not result in symmetry as it does in *A. richardsoni*. It is also of interest to note that one specimen of *Dictyonema flabelliforme* is known which shows signs of regeneration, and the regenerated portion, although lacking the regularity of the proximal end, nevertheless reverts to a branching frequency approximating to that of the proximal end of the rhabdosome (Fig. 3A).

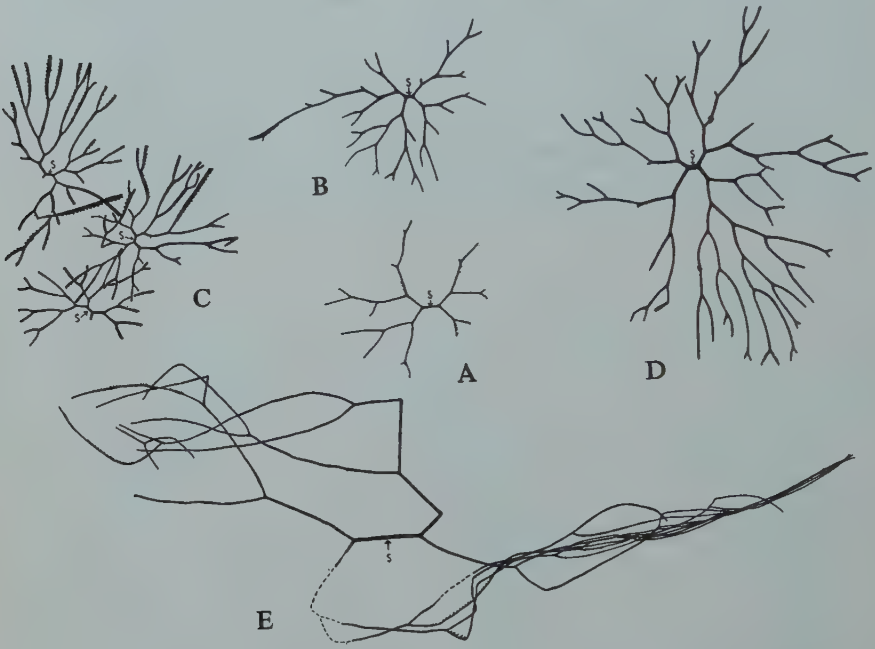

Fig. 2.—Rhabdosome form in some *Clonograptus* species showing different branching frequencies. The rhabdosomes are all partly damaged or imperfectly exposed and have not been restored. A, *C. tenellus tenellus* Linnarsson, B, *C. tenellus callavei* (Lapworth) (Tremadocian Sweden) ; C, *C. flexilis* (Hall), D, *C, rigidus* (Hall) (Lower Ordovician, Canada) ; E, *C. ramulosus* Harris & Thomas (Lower Ordovician, Australia). A–D, × ½, E, × ¼. *S* marks the position of the sicula, the growth centre and point of suspension of the colony. From Westergård 1909, Hall, 1865, and Harris & Thomas, 1938.

In the true graptolites, only one type of theca is present and branching must be due to the periodic formation of two zooidal buds in place of the normal one. In relation to the dendroids, there is a break here in the evolutionary sequence which we still lack suitably-preserved material to investigate; and there is as yet no detailed information on the relations of the two thecal buds to the parent theca except in *Tetragraptus bigsbyi* (Fig. 1F). But the true graptolites often exhibit a comparable regularity in rhabdosome form, implying that here too all growing points of the rhabdosome reacted similarly and more or less simultaneously; as in the anisograptids, the spacing of branching nodes is a specific character. Both true graptolites and anisograptids were presumably suspended from floating seaweed by the nema, and were able to develop freely in all directions. Balance about the point of suspension would be maintained by regularity in branching, but the frequency appears to be a specific character.

One of the most striking features about the succession of graptolite faunas throughout the Lower Palaeozoic is the general replacement of many-branched by few-branched colonies; multiramous dichograptids are virtually confined to the lower part of the Ordovician, unbranched bilateral rhabdosomes or the single-stiped biserial diplograptids predominate in the Middle and Upper Ordovician, while single-stiped uniserial monograptids entirely dominate the Silurian. The branching process therefore assumes real phyletic importance in the Graptoloidea. Reduction to a two-stiped (*Didymograptus*) stage may be through a centripetal decline in the power of dichotomy, as represented by the series: multiramous → 8-stiped (*Dichograptus*) → 4-stiped (*Tetragraptus*) → 2-stiped (*Didymograptus*); though it is also probable that many species of *Didymograptus* and *Tetragraptus* have arisen directly from multiramous ancestors by an abrupt failure of all but the earliest dichotomies through a sort of "colonial neoteny". With the attainment of the unbranched bilateral rhabdosome (*Didymograptus, Leptograptus, Dicellograptus* etc.) a state of considerable

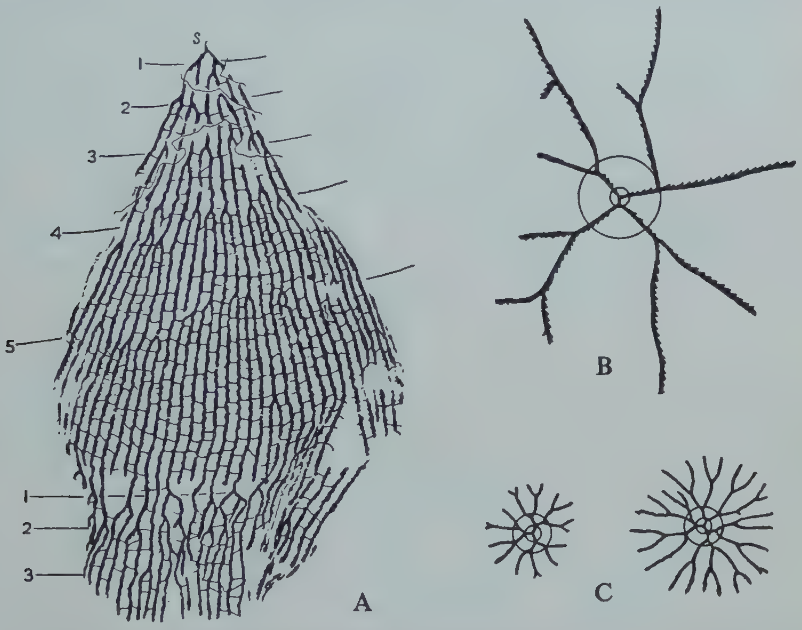

Fig. 3.—A, *Dictyonema flabelliforme* (Eichwald) (Tremadocian, Shropshire) showing regeneration in distal portion of the rhabdosome. S = sicula; 1, 2, 3 etc. mark positions of the approximate zones of branching. B, *Anisograptus matanensis* Ruedemann (Tremadocian Canada); circles drawn round the sicula at 1 and 5 mm. C, Two growth stages of *A. richardsoni* Bulman (Tremadocian, Canada); circles drawn round the sicula at 1 and 2½ mm. All figures × 1.

morphological stability is reached, and only one " double bud " is produced during the course of rhabdosome development.[1]

The Proximal End in Diplograptids.

The origin of the biserial diplograptids is one of the unsolved problems of graptolite phylogeny. Their earliest representative, *Glyptograptus dentatus*, occurs in the Arenig of Britain ; by Llanvirn times, it and its descendants are almost world-wide in distribution ; and throughout the Middle Ordovician, biserial graptolites steadily increase in numbers and importance.

At the proximal end of the typical biserial graptolite, the first three thecae (*th*1^1, *th*1^2 and *th*2^1) are alternating in origin, but the third theca (*th*2^1) produces two buds (*th*2^2 and *th*3^1) which stand at the base of two linear series of thecae separated by a median septum (Fig. 4). Even in the bilateral rhabdosomes of dichograptids, leptograptids and dicellograptids, there is a tendency to delay the formation of this " double bud " from *th*1^1 to *th*1^2 and from *th*1^2 to *th*2^1, but there the process goes no further (Fig. 4). With the establishment of the scandent biserial rhabdosome, it can and does proceed further, the generation of the " double bud " being deferred from *th*2^1 to *th*2^2, *th*3^1 or any later theca, and more and more of the early thecae alternate in origin. In some diplograptids, the entire rhabdosome consists of alternating thecae

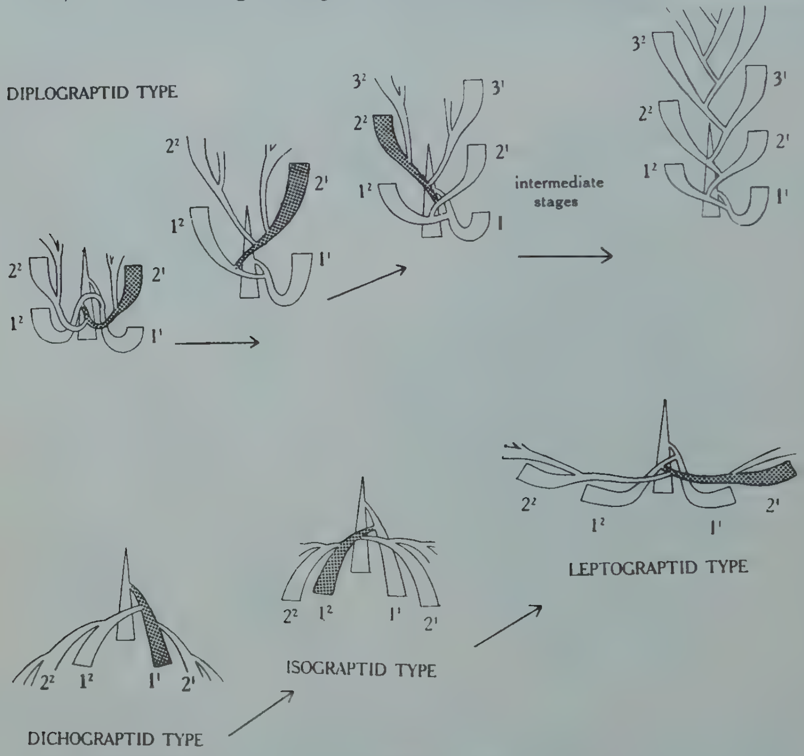

Fig. 4.—Thecal diagrams showing the mode of development of the proximal end of the rhabdosome and relations of the early thecae in dichograptid, isograptid, leptograptid and diplograptid types of development. The thecae carrying the " double bud " are indicated by stipple.

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[1] I am leaving out of consideration here the so-called branched leptograptids. Their branching is lateral, not dichotomous, and its details are completely unknown ; it may prove to be in the nature of cladial development (see later). The ancestry of these forms and their relation to lateral-branched dichograptids is also uncertain.

and there is no median septum. The diplograptid fauna as a whole is not affected by this trend—there are numerous late Ordovician and Silurian diplograptids with a complete septum—but it affects side lines repeatedly, and, for example, the point of origin of the septum in the varieties of *Climacograptus scalaris* can be used as a zonal indicator. It would seem that the tendency of the early Ordovician graptolites to eliminate branching divisions is here expressed in a rather different way.

Thecal Variation in Monograptids.

The ultimate limit of simplification in form of the graptolite rhabdosome is reached in the Silurian with the unbranched, uniserial, scandent rhabdosome of the monograptids. Here again, the origin of the rhabdosome type was sudden and its mode of evolution is still a matter of speculation ; but at no stage during development now is a " double bud " ever produced. Nevertheless such a rhabdosome may exhibit a very distinct pattern of a different sort, due to a regular variation in the form of the constituent thecae along the branch.

Among Dendroidea, the form of the autothecae throughout the rhabdosome is uniform for any particular species, and the whole range of variation throughout the order is not particularly great, though the bithecae show rather more and perhaps capricious variability. With the origin of the Graptoloidea, a new feature is seen : the thecae exhibit a regular increase in size to a specific maximum, so that the branches are of uniform width only in their mature portions. Among the Dichograptidae, with their characteristically simple, tubular thecae, there is little further differentiation, but other families may exhibit a wide range of variation in the shape of the thecae in a colony. This feature has been investigated more closely in the Monograptidae but is by no means confined to this family ; dicellograptids, dicranograptids and diplograptids all provide examples.

Such variation is absolutely regular, and is a striking if not unique feature of the colonial development of graptolites ; apart from a few pathological specimens, irregular thecal variation is unknown. The available evidence suggests that new types of thecae appear at the proximal end of the rhabdosome, gradually losing their distinctive character as the colony grows to maturity ; and that in a phyletic series, the new types spread further and further along the rhabdosome. Westoll (1950) has linked this phyletic change in form with increase in thecal size, suggesting that in early members of the " hooked trend ", for example, the whole series of thecae (Fig. 5B) could be regarded as potentially hooked if the thecae could grow large enough. This " potential hypermorph " concept appears at first sight to offer an attractive explanation of the remarkable " katagenetic " members of the hooked trend (*M*. cf. *colonus*), but it ignores certain differences in prothecal and metathecal form and it is by no means certain that it can apply even here ; in the isolate and triangulate " lines " (Fig. 6) the whole shape of the thecae (prothecal and metathecal portions alike) changes progressively, and the operation of some factor of gradually decreasing intensity throughout the colonial unit appears a more probable explanation.

Cladia Formation in the Cyrtograptids.

In Middle Silurian (Wenlock) times, a new rhabdosome pattern appears with the " pseudo-branched " monograptid, *Cyrtograptus*. Since the " branches " or cladia are themselves scandent and possessed of a virgula, they are clearly not true branches : but their detailed structure and mode of development have only recently been made known through Thorsteinsson's work on Canadian material dissolved out of a limestone matrix. At present, details have been published only for *C. rigidus* with its solitary cladium, but he has claimed that the underlying principles are equally applicable to species with a more complicated pattern of growth.

Each cladium originates at the aperture of a theca on the parent rhabdosome as a tubular outgrowth, accompanied by the development of a secondary lateral aperture

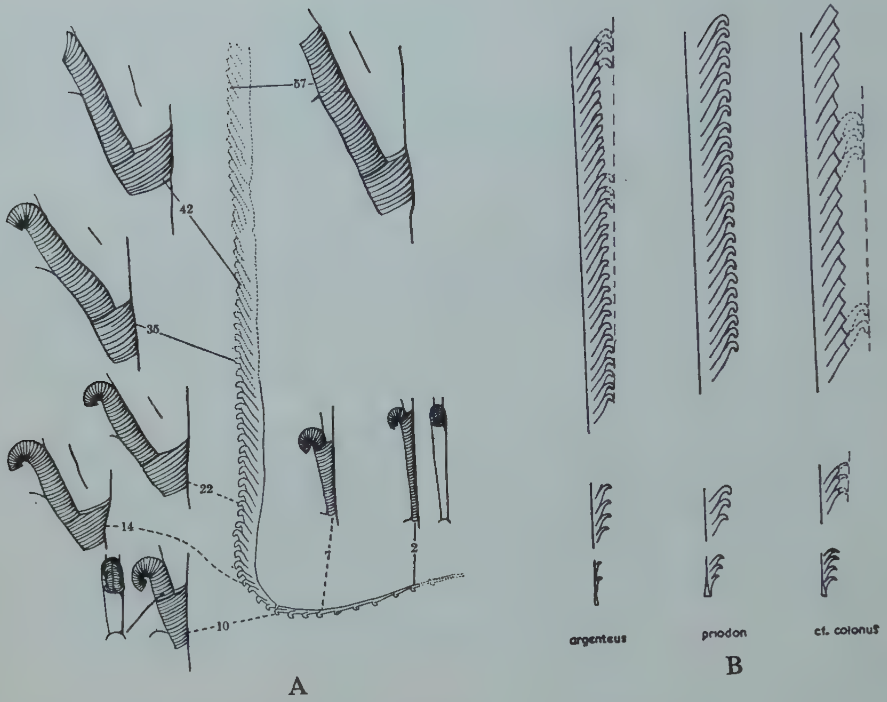

Fig. 5.—Thecal variation in monograptids.

A *Monograptus argenteus* (Nicholson) (Lower Silurian) showing progressive change in form of the thecae through the rhabdosome. This species is regarded as one in which the hooked type of theca is being introduced at the proximal end. Outline figure represents the entire rhabdosome × 2; individual thecae are restorations × 10 in full relief, based on pyritized specimens. Growth lines partly conjectural (from Bulman, 1951). B, Diagram illustrating the explanation of the introduction and loss of hooked thecae in the *priodon* series on the " potential hypermorph " concept (from Westoll, 1950).

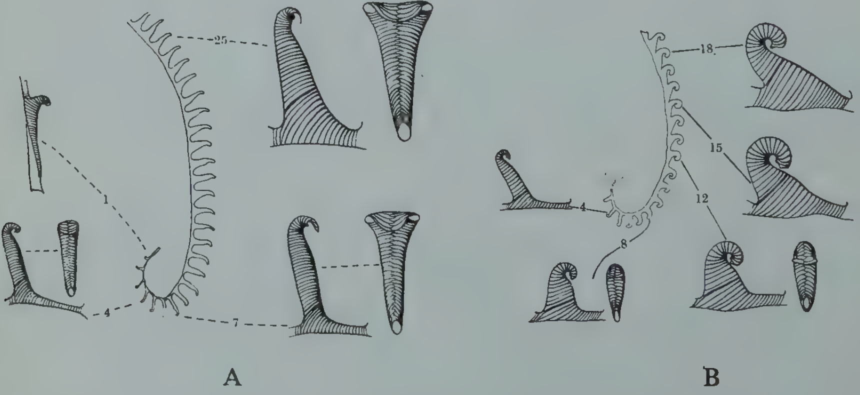

Fig. 6.—Thecal variation in monograptids.

A, *M. triangulatus* (Harkness), B, *M. denticulatus* Törnquist (Lower Silurian). Outline figure represents nearly complete rhabdosome × 2; individual thecae in full relief, × 10; growth lines partly (*triangulatus*) or largely (*denticulatus*) conjectural (from Bulman, 1951).

to the mother theca. Until the production of its cladium, there is nothing to distinguish the mother theca from any other theca on the main stipe, but for many species the position of the mother theca (reckoned from the proximal end) is nearly constant, and if more than one cladium is present in the adult of the species, their spacing is regular[2]. The first signs of a developing cladium become visible in *C. rigidus* on *th*9 (± 1) when the main stipe has developed to *th*13 (± 1), and its earliest developmental stages occupy a time represented by the addition of three or four more thecae, so that the first thecal segment of the cladium is completed only when the main stipe has reached *th*16 (± 1). In other words, the cladium does not start to develop until some three or four thecae have budded off distally to the mother theca, and an additional three or four grow on the main branch during the completion of the first thecal segment of the cladium.

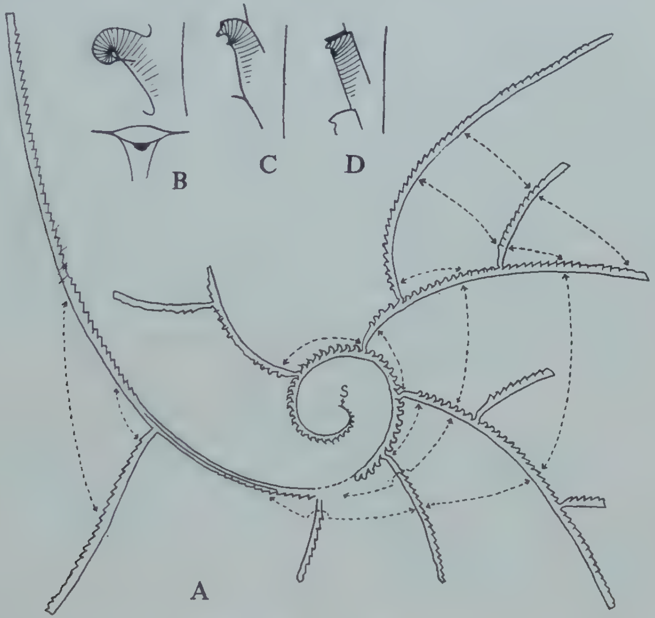

Fig. 7.—A complex *Cyrtograptus* (Middle Silurian) with cladia of two orders. Approximately contemporaneous thecae are connected by broken lines. × 1. *s*, Sicula. B, C, D, diagrammatic enlargements to illustrate differences between the form of the thecae from the proximal (B), middle (C) and distal (D) portions of the rhabdosome.

Progressive change in thecal form is usual in the cyrtograptids and the shape of the first cladial theca corresponds closely to that of the contemporary theca on the main stipe. Thereafter, thecae are added to both at the same rate, and progressive change in the main stipe thecae is paralleled in the thecae of the cladium, so that at any time thecae of the same type (same size and form) are being added at both the growing ends of the composite rhabdosome. Thorsteinsson's material includes many complex cyrtograptids, and he claims that this intimate relation applies equally to those with several cladia and even to those with cladia of two or more orders (Fig. 7). This means that in a complex cyrtograptid, comparable gradually changing thecae are being added, by asexual budding, to each of many separate growing points of the colony.

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[2] There seems to be some variation in European material, though the subject has not been systematically investigated ; but in the rich and beautifully preserved material from northern Canada, Thorsteinsson claims (*in litt.*) that the positioning of the cladia is remarkably regular and in some species perfectly constant.

Summary.

The examples of rhabdosome development described above clearly suggest that the graptolite colony is far from being a haphazard aggregate of individuals, but behaves as a complex unit of which the pattern is often precisely regulated. This regulation, which is effected through the budded succession of individuals, appears as something comparable with the varying field of growth potential of a solitary organism and perhaps finds its closest parallel among metamerically segmented animals.

Branched rhabdosomes typically show great regularity and symmetry in the disposition of their branches, whether these result from the periodic substitution of a stolotheca for a bitheca (as in siculate dendroids) or the production of two buds in place of the normal one bud. All growing points of the rhabdosome react more or less simultaneously and the frequency with which divisions occur is recognized as a specific character. There is commonly a steady decrease in branching potential as the colony approaches maturity and the regularity becomes noticeably less in higher " orders " of branching. Simplification of the rhabdosome by reduction in the number of branches is a " trend " affecting the whole order Graptoloidea, resulting ultimately in the production of a single chain of a limited number of individual zooids.

Distinctive also of the Graptoloidea is a regular and progressive variation in the form of the thecae through the colony. In certain species, these changes are mainly in proportion, such as could possibly be related on a growth gradient to absolute size and length of development, but the majority involve a definite change in shape transmitted through a linear budding series. This thecal pattern finds its most complicated expression in the cyrtograptids, where cladia are developed from certain of the thecae after an appreciable lapse of time and yet the change in thecal type in the main branch appears to affect sympathetically and more or less simultaneously all the growing points of many successive cladia.

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TRANSFERENCE OF FUNCTION

By E. J. H. Corner, F.R.S.
(*Botany School, Cambridge.*)

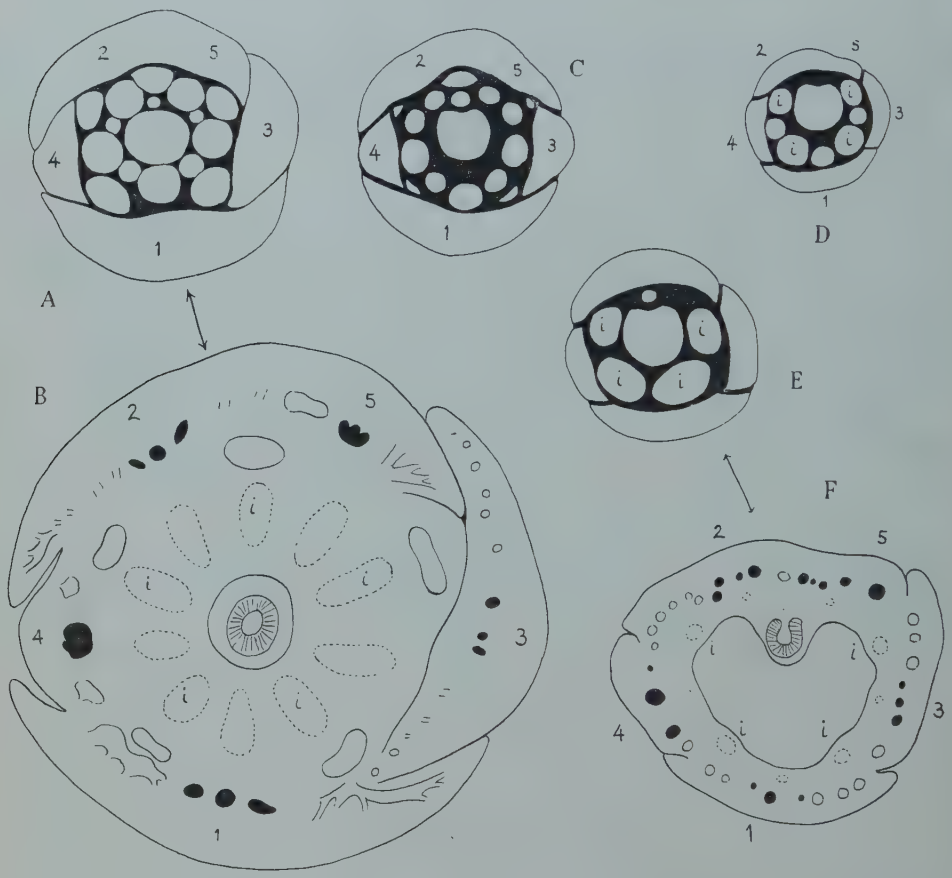
(With 2 text-figures.)

The systematic comparison of plants, and probably of animals, shows that a property which occurs in an organ, tissue, or cell-layer in one case may occur in other parts of the body in other cases. The property is the same, but its site of development has shifted. These deviations are found at all levels of classification; the transference of function, therefore, as I have called the process (Corner, 1949*a*, p. 381; 1949*b*, p. 360) is a method of evolution.

A simple example is the presence of anthocyanin in the flowering-plant. At some stage in development, the colour appears. In one variety the underside of the leaf may be red, or merely the veins, or the petiole or node or internode, or the colour may appear only in young leaves or old leaves, or only on insolated surfaces. Such small differences are usually passed over, though of horticultural value; yet, they raise the question why one part of the epidermis should be different from another. There is not just the property to be considered, but the site of its materialization. Presumably the property is inherent in all the cells, but only in certain parts of the body do the circumstances evoke it. A hereditary character consists of two parts, the property and, what must be more complex, the conditions which materialize it. Thus I understand the evolution of the property as anagenesis in the first place, and the diversification or cladogenesis of its occurrence. Stasigenesis of Huxley (1957) is shown by the widespread pigmentation of petals rather than sepals. When, with the loss of petals, the calyx becomes pigmented, there is a profound modification of floral organization, as Miss Saunders (1933) has explained. A remarkable instance is *Saraca* (Leguminosae-Caesalpinioideae-Amherstieae). Its petals are lost; the tetramerous calyx takes their function and their vascular supply; the inner whorl of stamens takes the place of the petals; and the outer whorl of stamens is variously reduced (Text-fig. 1). *S. thaipingensis* Cantley ex King has the effective formula K4 CO AO + 4, but the full vascular supply K5 C5 A5 + 5, the petal-bundles lying in the sepals and the bundles of the undeveloped stamens ending blindly in the receptacle (Rao & Sirdeshmukh, 1954). The derivation of this flower can be traced through other species and such allied genera as *Pahudia*, in which the four petals, other than the standard, soon abort and the inner stamens encroach upon their positions. There is no metaphysical problem whether sepals are homologous with petals or petals with stamens or whether any of them are defined by vascular bundles; indeed, there is nothing new in this flower but the transference of function from one part to another and degeneration characteristic of the zygomorphy of the tribe. Yet, the transference of colour is here the outward sign of intensive evolution.

Floral Examples.

Most cruciferous inflorescences have no bracts, save at the beginning of the raceme. The bracts can be traced on the stem-apex as inhibited leaves. As the inflorescence develops, the inhibition increases; the flower-primordia occur at first in the axils of microscopic bracts, and then the primordia which should become bracts become flower-buds directly. That is, the stem- (inflorescence-) apex produces in phyllotaxis not leaves (bracts) but stems (flower-buds) without attendant leaves. Here, again, there is no metaphysical problem such as whether a phyllome-system is turning into a telome-system or a cruciferous inflorescence is not homologous with a vegetative shoot, but a direct and observable transference of the properties of engendering a flower-bud from the axillary position to the primary primordial position. I write observable because it can be seen in a few minutes on dissecting the young inflorescence of *Capsella* under the binocular microscope, which I take as my first practical in advanced taxonomy; it is not in the books. Nevertheless, the same process must occur in composite capitula and aroid spadices without interfloral bracts, though so subtly as scarcely to excite remark. The process must be the explanation, at least in part, of the notable epiphyllous flowers borne on mid-ribs (Stork, 1956).



TEXT-FIG. 1.—Leguminosae- Caesalpinioideae- Amherstieae.

Flower-buds showing the primordia of petals, stamens and ovary (central), the sepals cut off but numbered in order of development (2 and 5 connate), × 50.

Sections of full-grown flower-buds at the level of insertion of the sepals to show the sepal *v.b.* (black), the petal *v.b.* and their sepaline derivatives (white), the staminal *v.b.* (dotted), and the ovary *v.b.* (hatched), × 15.

A, B, *Hymenaea courbaril* L. (K4 C5 A5 + 5): C, *Pahudia rhomboidea* Prain (K4 C1 A3 + 4): D, *Saraca declinata* Miq. (K4 C0 A3 + 4): E, F, *Saraca thaipingensis* Cantley ex King (K4 C0 A 0 + 4); the inner whorl of stamens (*i*).

Condensed inflorescences simulate single flowers. Outer bracts resemble sepals, inner bracts or neuter flowers petals, male flowers stamens, and central fruiting florets carpels. Such inflorescences are condensed because there is no internodal extension (that of the female flower in *Euphorbia* simulating the gynophore), and on the broadened inflorescence-apex the many small flowers are crowded. It is under conditions of complicated proximity that transference of function is to be expected; the circumstances under which properties materialize are there likely to overlap. There is, again, no need to appeal to a metaphysical floral " Gestalt ", but to perceive the way in which floral properties precociously pervade the stem-apex co-extensively with inflorescence properties. Such inflorescence-flowers, in fact, affirm the floral properties by transferring them to the greater scale of the inflorescence. A precise example is afforded by *Parkia* (Leguminosae-Mimosoideae). In the Amazonian section Paryphosphaera (Ducke, 1938), the large clavate capitulum has sterile, petaloid basal flowers, then many functional male flowers, and about a dozen apical perfect flowers which set individual pods. The compound fruit of *Parkia* resembles in its inflorescence-stalk, head, and bunch of pods the simple fruit of *Archidendron*, of the same subfamily, where the pods are from the numerous carpels of the one flower. *Archidendron* has simple capitula without transference of floral properties, but *Pentaclethra*, allied with *Parkia*, with petaloid stamens is in some measure intermediate; it shows how the steps in cladogenesis may be revealed by allied genera.

The syncarpous ovary has always been a problem, now beset with many artificial theories. In essence it is an intercalary growth at the base of the free or apocarpous carpel-primordia, which thus become elevated on the new " ovary-box ". This seems a new feature, but it is merely concerted internodal growth. However, the point is that most of the properties of the apocarpous ovary become transferred to the new intercalation, namely the placentas with the ovules, the vascular supply, the post-fertilization development of the carpel-wall and the method of dehiscence. This has led to the quibble about the number of carpels in the syncarpous ovary, which is a misnomer without carpels, though the functions of the original carpels have been transferred to it in a manner suggesting the fallacious idea of fused carpels. The positions of the placentas may also be transferred within the syncarpous ovary (Puri, 1952), ending in the single terminal ovule, as in Gramineae. Then in the inferior ovary, the original carpel-functions are variously transferred to the receptacular tissue, or sepal-internodes, particularly the post-fertilization development of the ovary-wall into the fruit. These well-known, but too often mis-stated, modifications of the flower show how the transference of function puts orthodox morphology into the state of flux in which teratological phenomena are the exaggeration. In floral morphology, on which phylogenetic classification so much depends, it is necessary to formulate an archetype and to define both its properties and their spatial dispositions, as Wardlaw has recommended (1956), in order to follow the diversification caused by transference of these functions to new regions of intercalary growth. These regions, such as the corolla-tube and receptacular tube, may be minor steps in anagenesis, but their polyphyletic parallelism implies rather that they are also transferences of meristematic activity from apical to basal regions of primordia; the intercalated regions of the flower do not add anything really new to floral construction. The diversification, or cladogenesis, of both flower and fruit seems, therefore, to have been largely the transference of the functions of the original free primordia to the receptacle or parent stem, the acorn being a crowning achievement.

Fruit Examples.

As just mentioned, the properties of the syncarpous superior fruit are transferred to the receptacular wall of the inferior fruit. Fleshy peduncles and fleshy sepals seem to be similar examples of the transference of fruit-fleshiness, the primitiveness of which I have argued elsewhere (Corner, 1949*a*, and 1953). Thus, the fleshy peduncle and dry nut of the cashew (*Anacardium*) is a mango with the pulpy property of the pericarp transferred to the fruiting peduncle: experiments with strawberries (*Fragaria*) suggest that here, too, the cause may be the change in site of the receptor of the hormonic stimulus emanating from the developing embryo. In fleshy inflorescence-fruits, such as pineapple, pandan, breadfruit, and fig, complicated transferences of pulpy and sclerotic layers occur, recalling the transference of flower-properties in inflorescence flowers. In the Moraceae, the original fruit seems to have been a drupe, the fleshiness of which has generally been transferred to the sepals, as in the mulberry (*Morus*), or to the inflorescence-axis as in some of the breadfruit-allies and in the figs. The fruit of *Carludovica* shows transferences of the palm-fruit properties, paralleled by *Monstera* in the Araceae. Similar to the Moraceae, is the case of *Pernettya* and *Gaultheria* in the Ericaceae, *Pernettya* having the fleshy pericarp and thin calyx, *Gaultheria* the fleshy calyx and thin pericarp ; in *Vaccinium* the receptacle is fleshy, as the inferior berry. In *Ricotia* (Cruciferae) the pods may contain winged seeds or the pod may be indehiscent and winged. *Sterculia alata* Roxb. has winged seeds and in the allied *Tarrietia* it is the one-seeded pods which are similarly winged. In the rhubarbs (*Rheum*) the fruit is winged along the three angles, but in the docks (*Rumex*) it is the persistent sepals, not the three-angled fruit, which may be winged. The position of the viscin-layer in the Loranthaceae, according to Danser (1931), is either outside the vascular bundles (Loranthoideae) or inside (Viscoideae), suggesting transference from some ancestral position.

There are many analogies between fruit and seed in allied plants which must express transference of function, and, be it noted, this transference, as with inflorescence-flowers, seems always to be from the central or apical region towards the the basal as though the disturbing influence came from below and the centre was left solely with the function of embryo-development. Thus, division of labour is but an aspect of the process.

Seed examples.

It was the study of the intricate microscopic structure of the coats of large seeds which brought this whole problem to my attention, where fortunately there had been no theory to obscure the facts. The annonaceous seed-coat, developed from the outer integument, has, besides layers of crossed fibres, cell-layers with crystals and cell-layers with oil-cells, both of which vary in position in different genera, but the most remarkable transference occurs in those genera with a middle, or fourth, integument (Corner, 1949*a*, pp. 360–361). The middle integument develops after fertilization and it, alone, has the characteristic fibres and crystal-cells. It seems that the normal differentiation of the outer integument is here transferred entirely to the new integument and that there is not merely the transference from one normal structure to another, though this, too, occurs abundantly. Thus, the palisade-layer of columnar Malpighian cells (macrosclereids) occurs in different positions. In several families, of which the Leguminosae are the best example, the layer is the outer epidermis of the outer integument (Corner, 1951). In the Cucurbitaceae the layer is hypodermal (Singh, 1953). In Myristicaceae it is the inner epidermis of the outer integument. In many others, as the Bombacaceae, Malvaceae, Tiliaceae, Sterculiaceae (Venkata Rao, 1950), Euphorbiaceae (Singh, 1954), Bixaceae and Celastraceae, it is the outer epidermis of the inner integument. The property appears to be the same in all, but its position differs.

I extended the principle to the aril and its derivatives, arguing that the sarcotesta, or fleshy seed-coat, which is so often associated with degenerate arils, might not be merely the undifferentiated testa, but one to which primitive aril-properties have been transferred (Corner, 1949*b*, 1953). Objections have been raised by van der Pijl who maintains the converse that the primitive properties of the sarcotesta, as found in pteridosperms and gymnosperms, have been transferred to the aril as a new outgrowth, similar, I suppose, to the middle integument of the Annonaceae (v.d. Pijl, 1955, especially fig. 1, p. 59, and 1956). Our disagreement arises from the two legs of evolutionary theory, the palaeontological and the living, and I am not persuaded by inference from pteridosperms either that angiosperms must have been derived from them or that the sarcotesta of *Magnolia* is primitive or homologous with that of

Cycas. For the present my point is to show that, in order to write this great chapter of plant-morphology on the evolution of the seed, the extreme intricacy of the structure demands analysis into properties, sites and transfers. The aril, itself, exemplifies the transfers because it may arise from several different parts of the seed, as from the funicle-apex (Leguminosae, Dilleniaceae, Papaveraceae), and the micropyle also (Annonaceae, Nymphaeaceae, Myristicaceae, Bombacaceae, Celastraceae, Sapindaceae), from the chalaza and not the funicle (Connaraceae, Meliaceae, Elaeocarpaceae), and from the side of the seed opposite to the chalaza (*Leptonychia*).

Regarding strict embryology, it seems that the varying division of labour among the cells of the early embryo, which form cotyledon, radicle and stem, results from transference of functions in different species of a genus, or genera of a family. The complete inversion of the embryo of *Sterculia* may be a reversal of polarity. Hypocotyl embryos, too, in which food is stored in the hypocotyl, must be regarded as transferences from the cotyledonary position, or conversely, e.g. *Anisophyllea*, *Barringtonia*, *Bertholletia*, *Garcinia*, *Ternstroemia*, and, perhaps, *Rhizophora*.

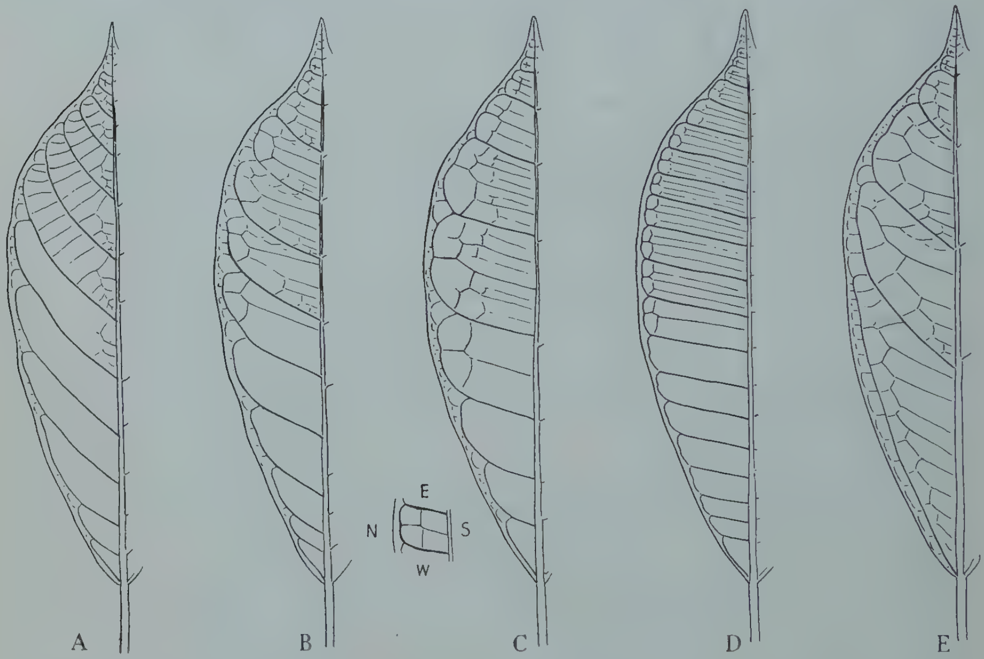
Shoot Examples.

Yet another " Gestalt ", which can be understood, is the resemblance of branch-systems to pinnate leaves. It is most striking in the Phyllantheae (Euphorbiaceae), which seem to have simply or doubly pinnate leaves, for those on the main stems are reduced to minute scales, and the leafy branches have limited growth (Corner, 1940, pp. 278–280). It seems that the form-factors, or properties, of the pinnate leaf have been transferred to the axillary buds of the main stem on the degeneration of their own leaves. But, in the Euphorbiaceae, and also in Flacourtiaceae (*Casearia*, *Hydnocarpus*), where the same phenomenon occurs, no pinnate leaves are known, though simple leaves may show pinnate lobing. In such cases one cannot dismiss the pinnate construction of the leaf itself, as shown in its venation, from being the physiological basis of the phyllomorphic branch : these genes must exist in the plants and may as well operate in the axillary buds, just as those of the flowers in *Capsella* operate in the leaf-primordia.

Normally the plumule of the seedling becomes the main stem. In many Papilionaceae the plumule has limited growth, or even degenerates in the seed, and the axillary buds of the cotyledons take over the function of the main stem (Dormer, 1945). This is an extreme case of sympodial growth, which is variously developed in plants so as to cause substituting growth of the leader when it dies. Probably there is some fairly simple hormonic control, but such cases show how variations in the site where functions materialize affect the form of the plant. In the epiphytic orchid *Taeniophyllum* there is no vegetative shoot, but a minute inflorescence, and the green strap-shaped roots take over the physiological functions of the shoot. The mechanism of photosynthesis is, presumably, no different from that in the leaves of other orchids, but it has been transferred entirely to the roots. Green roots, occur, of course, in many orchids, and comparative taxonomy will show how gradual must have been the change over to the state in *Taeniophyllum*. Thus, it seems possible to explain the well-known case of *Streptocarpus* (Gesneriaceae), in which a single and much enlarged cotyledon bears the flowers and, even, the roots, in terms of transference of all functions to the cotyledon. Should we not, indeed, conclude that the secret of angiosperm success lay in this facility of transfer ?

Leaf Examples.

A simple dicotyledonous leaf has normally pinnate venation, the numerous side veins being largest where the leaf is broadest. Some leaves, however, have the basal pair of side-veins prolonged, even to the leaf-apex (Text-fig. 2E). Such are the triplinerved leaves of gentians, Caryophyllaceae, Melastomataceae, and others. The lamina develops only in the basal part of the leaf-primordium between the first and second pair of side-veins, for in the tip of the expanded leaf the other side-veins may still be found unextended. All the intercalary growth of the lamina, which makes the mesophyll between the veins, has been transferred to the interval between the first and second pairs of side-veins, It is known that there are two processes, at least, in leaf-growth, one making the veins and the other the filling between them, as shown by the skeletal spring leaves of the horse-radish followed by normal summer leaves. Phyllodic leaves, with many subparallel longitudinal veins, as in the plantains (*Plantago*), are interpreted as petioles or leaf-bases extended to form a lamina, and this is mesophyll development transferred to the intercalary growing region at the base of the leaf-primordium. In *Lathyrus* the leaf is pinnate with distal tendrils as non-laminate pinnae : a few species have pinnately veined leaflets, but most have phyllodic leaflets, and some have no leaflets but phyllodic petioles or foliose stipules. Thus, in one genus, there can be traced the transfer of lamina-formation from the normal position to the leaf-base, whence it may descend to the internode and give the winged stem and cladode. That is why I regard such leafless, leaf-stemmed plants as cacti as plants, not so much with dislocated chromosomes, but with dislocated sites for gene-activity.



TEXT-FIG. 2.—*Ficus*-leaves of similar shape but different venation, showing mid-ribs, costas (main lateral veins) and main intercostal veins. *Inset*, the primary subdivision of the intercostal area by two veins NS and EW, as visible near the tips of the leaves.

A (*F. annulata* Bl.), parallel intercostals from NE quadrant; B (*F. globosa* Bl.) cascade vein from SW quadrant ; C (*F. vasculosa* Wall.) all quadrants developed ; D (*F. elastica* Roxb.) SW and SE quadrants predominant ; E (*F. indica* L.) as B, but triplinerved.

A more subtle process concerns the details of venation. In *Ficus*, and many other plants, the mesophyll may develop in different ways between the side-veins. At first, a sort of square develops between a pair of side-veins, to be divided by secondary veins into four quasi-squares (Text-fig. 2, inset). Generally the distal square (NE) develops most to form many cross-veins (Text-fig. 2A), the other three remaining little changed. In *F. elastica* Roxb., the two squares (SE and SW) next the mid-rib develop to form the lamina (Text-fig. 2D). In *F. indica* L., it is the proximal square (SW) which develops most to form a sort of cascade-vein into the axil of the lower side-vein (Text-fig. 2BE). And in other species, all the squares develop evenly (Text-fig. 2C). In *Lactuca, Camellia, Diospyros,* and others the mesophyll develops largely outside the inarchings of the main side-veins to give several series of loops. Whatever the primitive venation of the dicotyledon, it is varied by transference of mesophyll development to certain parts to give the characteristic adult venation so hard to describe until explained, and this explanation is often to be found on tracing the manner in which the venation simplifies, or closes up, towards the apex of the adult leaf (Text-fig. 2).

Lastly, I would recall the pitcher leaf of *Nepenthes,* which exhibits a basipetally developed, or reverse, explanation of leaf-properties. It has a phyllodic, photosynthetic, winged petiole, the wings decurrent on the stem ; an intermediate, thigmotropic, tendril-stalk without lamina ; a secretory and absorptive, basipetally developed, pitcher as the lamina-base (so often glandular in other plants) ; and, apically, the rest of the reduced lamina as the convenient lid, which is the first part to be developed. Instead of being combined into one unit, as in *Clematis,* the leaf-properties are here displayed. The experimental challenge is their recombination into the pre-*Nepenthes* leaf.

Examples from Classes other than Angiosperms.

I have taken examples from flowering plants, but the principle extends to other classes. It must enter the morphology of gymnosperm cones and embryos, the disposition of fern-sori and annuli, peristome variations in mosses, hymenial configuration in basidiomycetes, spore-forms in rusts, and sporangial disposition, meristematic variation, and, even, life-cycle differences in algae, such as the difference between the generations in *Cutleria, Laminaria* and *Dictyota.* But, in the algae, we encounter the principle of division of labour. If reproductive cells are set apart from vegetative, the underlying process of this division of labour must be the transfer of reproduction to those cells which evoke the reproductive metabolism. On the other hand, if the lower cell of a two-celled embryo forms the attachment, external, not internal, stimuli may be the cause. As Church has shown (1920), the organization of algae is so intimately connected with the external environment that it may not be possible to decide by inspection whether a property is facultative and disperse, that is materializable in many parts of the soma, or genetically localized. That the large sporophyte of Laminaria may be reduced to a few cells in artificial culture is a warning against speculation. In contrast, the emancipation of the higher plant has depended as with the animal on the evolution of the internal environment.

Neoteny.

A function is transferred by moving the site in which the inherited property materializes. The mutation, if any, affects the conditions for materialization. The change may allow the property to develop earlier than usual, when it may affect a wider, smaller, or different region of the body. Thus homaeosis, or " the earlier incidence of a morphogenetic process " (Goldschmidt, 1938), may arise, and, also, neoteny or the precocious maturity of an organ or organism so that it functions in an otherwise undeveloped state. It is likely that transferences of function occur at developmental stages different from the original, so that both neoteny and " gerontoteny " are but aspects of the one principle. The importance of neoteny is widely acknowledged. I had occasion to refer to it as " juvenescence " when considering the evolution of the fruit-body in discomycetes (Corner, 1930). It seems to be the process which has separated pollination from seed-shedding and given the precocious flower-bud to be followed by fruit-setting, and also the smaller and simpler flower.

It is the process which has derived *Lemna*, as the floating aroid seedling, and the annual herb. What is required of the systematic morphologist is the evaluation of properties, which Church called factors of equipment, and a hypothesis of their original state and subsequent transfer, preparatory to experimental analysis, which is often too miscellaneous for evolutionary thought. The principle of transference of function is based upon structure, as the means for protoplasm to manifest itself by filling space and interacting with the environment, but it operates through physico-chemical processes. It transcends the particular disciplines of biology, and, if the capable botanist or zoologist be now the superman, it will require a team of collaborators for elucidation, but the key is with the taxonomist.

Summary.

It is considered that many evolutionary changes in plants, including the division of labour and neoteny, result from restricting the site of development of a hereditary property or by moving it to another part of the plant-body. This principle of transference of function is explained by examples from the flower (especially *Saraca*) fruit, seed, leaf, and venation (*Ficus*) of angiosperms. Systematic morphology should seek to define the original properties, their sites and their transfers.

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DARWINISM AND THE STUDY OF EVOLUTION IN NATURAL POPULATIONS

By E. B. Ford, F.R.S.

(*Genetic Laboratories, Department of Zoology, University Museum, Oxford.*)

The one hundredth anniversary of the Darwin-Wallace Lecture will be celebrated by the publication of many books and essays. These will presumably review the principle of natural selection historically and in relation to rival theories, as well as in the light of palaeontology, plant and animal distribution, cytology and genetics. Yet it is probable that in so great a body of centenary literature, less than its due share of attention will be given to the study of evolution in wild populations by means of observation and experiment. For though such techniques are of the very type which Darwin himself delighted to use, little work along these lines was attempted until twenty years ago, and even now it is not being carried out extensively.

A potent reason for this, though not the only one, is the fact that the frequency and extent to which natural populations are affected by large selective advantages and disadvantages has been greatly underestimated. This remained almost universally true for more than fifty years after Darwin's death, nor in this matter is the correct state of affairs at all widely recognized to-day.

R. A. Fisher's *Genetical Theory of Natural Selection* was, when it appeared in 1930, the greatest contribution to evolutionary thought since the publication of *The Origin of Species*. Yet that book is mainly concerned with the study of selective advantages up to 1 per cent. or so. To-day we know that provided certain definite, but widely occurring, conditions are fulfilled, selective advantages of 30 per cent. or more are frequent in wild populations : a consideration which opens up great possibilities for the study of evolution in progress. For such work can be undertaken as a short-term project if appropriate species with an annual, or shorter, life-cycle be selected for study, since a few generations suffice to demonstrate evolutionary changes when controlled by selection pressures of such magnitude.

It seems worthwhile, therefore, in this article briefly to review the conditions which facilitate rapid evolution in wild populations. Also to discuss some of the fallacies inherent in the non-selectionist interpretations which have from time to time been advanced to account for the changes to which they in fact give rise.

The study of continuous variation controlled on a polygenic basis will frequently reveal rapid evolution, or provide evidence of its recent occurrence, in a species subdivided into small isolated populations especially on the edge of its range. Quantitative characters of the kind here indicated can respond accurately to selection-pressure, owing to the large number, and small cumulative effects, of the genes controlling them. Thus when the population is split up into groups occupying restricted areas, each one can be adjusted to the ecology of its own habitat ; whereas when not thus subdivided, the species can be adapted only to the average conditions of an extensive terrain. Judged therefore by some measurable quantity, it should generally be found that isolated colonies when inhabiting several small areas will be more distinct from one another than when inhabiting several large ones.

This concept is exemplified by work on the butterfly *Maniola jurtina* in the Isles of Scilly. The character studied is the frequency-distribution of spotting on the underside of the hind wings in both sexes, but in this article that in the female will alone be discussed since this represents the simpler and more readily analysable situation.

Female spotting differs greatly from one to another of five small islands but is effectively similar on each of three large ones (16, see pp. 84–85 for frequency-diagrams); the difference in area between the two groups being seventeen times or more. Migration is excluded as an explanaton of the resemblance of the butterflies on the three large islands ; small islands with populations having different frequency-distributions being interposed between two of them, while the distances involved prove to be a complete barrier to this insect.

It might be thought that the dissimilarity of the populations on the five small islands is due to random genetic drift along the lines suggested by Sewell Wright (27). This supposition is completely excluded by their numbers. On the small island of Tean there are three of them, and they have been estimated as containing 15,000, 3000 and 500 individuals in a season respectively ; while the single population occupying the small island of St. Helen's must be considerably greater than the largest of those on Tean. Moreover, one of the Tean populations readjusted itself to a new spot-distribution in a single generation (the species has one brood per year) following a profound ecological change consequent upon the removal of a small herd of cattle (6). Work as yet unpublished shows the new type of spotting to be a stable one. Thus it is entirely controlled by selection.

Dobzhansky (4) has lately put forward an alternative view to the exclusively selective one advocated here. For he holds that the " founder principle " of Mayr (21) influences the effects of selection to produce the situation characterized by the *Maniola jurtina* populations in Scilly. He suggests that a few specimens reached and colonized the small islands " from other islands or from the mainland ". This, incidentally, is not historically a correct point of view, for the small islands have been progressively reduced in size since they were part of a continuous land mass only two or three thousand years ago. He holds that the genes which chance to be possessed by these hypothetical founders influence the effects of selection operating subsequently upon the populations derived from them. His suggestion follows from the results of a highly original experiment of his own work upon colonies of *Drosophila pseudoobscura* in population-cages. Some of these were derived from a few specimens (a foundation stock of 20 flies, 10 males and 10 females) while others were derived from many (4000 flies about equally male and female). Thus they were thought to represent the small island and the large island situations respectively. The parallel is, however, deceptive. The various population-cages had identical environments not in the least reflecting the great environmental differences from one to another island in Scilly, and allowing no assessment of the relative importance of the founder genes and of subsequent selection. The latter must in fact be overwhelming, such as to obliterate any " founder " effect. This might indeed influence the situation relative to a few major genes lacking from an original colonizing population. But the number of polygenes having similar and cumulative effects must be large (3) while the possible genetic diversity to which their segregation gives rise will be stupendous. Thus the effects of natural selection will wholly overweigh any others in the micro-evolution of these populations, and of this we have clear evidence. Not only did the ecological change due to the removal of cattle produce at once an evolutionary response in the *Maniola jurtina* population inhabiting a small island, but an ecological change of another kind has now done so as well on one of the large islands, Tresco. Here in 1957 a marked and heavily significant departure from the normal spotting of a large island has occurred for the first time within our experience in response to the ecological effects of a highly exceptional summer. In this matter, I am indebted to my colleagues for allowing me to mention results which we obtained together, the details of which are as yet unpublished. The fact that small and large island populations alike can change their characteristics markedly, in a single generation, and to an approximately equal extent, indicates how negligible must be the constitution of hypothetical founders compared with the working of selection.

The founder concept and that of random genetic drift are obviously inapplicable to the evolution of the vast populations of *Maniola jurtina*, often continuous over great areas, which inhabit the mainland. On the other hand, a purely selectionist interpretation of the situations encountered in them is as valid as upon small islands. Samples of the butterfly have been in a number of years collected from a large series of localities in southern England, from Devon to the North Sea, and southwards from Norfolk. These are from extremely diversified conditions : the Atlantic climate of west Devon and the semi-continental one of the Ispwich district, from alkaline and from acid soils with their widely differing ecology, as well as from sparse vegetation upon downlands and the luxuriant conditions of lowland meadows. Yet the female spot-distributions are similar in all of them, declining from a single large mode at 0 spots. Thus throughout this region they must be stabilized by selection, acting either directly upon the genes concerned or through a buffering of their effects. In central and eastern Cornwall, on the other hand, the insect is stabilized differently, with a mode at 0 spots and a second smaller one at 2. Already in 1952 we had found that these two areas of stabilization are, in the Launceston neighbourhood, separated only by 12 miles (5). It is now known that the species occurs throughout the intervening area ; it has been studied in detail there both in 1956 and 1957, with results which are at present being prepared for publication.

Further west in Cornwall, in the isthmus between Hayle and Marazion and eastwards thence for 10 miles or so, *Maniola jurtina* is rare or absent. This situation isolates two populations in the extreme west of the country. One of them occupies an entirely exceptional habitat on the Hayle sandhills : a strip along the north coast about four miles long and a few hundred yards wide. Here the population does not appear to be stabilized in regard to spotting. The second spreads sparsely over the Land's End peninsula, a granite intrusion of 75 square miles or so, where the spot-frequencies of the females take a constant value which differs from any other known on the mainland, having a single mode at 2 spots.

It will be noticed that a study of spots in *M. jurtina* has revealed both evolution in progress and adjustment to differing conditions. It will be realized that the genes which control this character must have other effects, presumably of a physiological kind, for which they are principally selected. Of these direct evidence is now being obtained from breeding experiments.

In Cornwall and the Isles of Scilly *Maniola jurtina* shows some of the characteristics of species at the edge of their range. These merit brief consideration both in the light of the present example and in terms of evolution in general.

An organism at the edge of its range is living in conditions which are either unfavourable or peculiar. In order to survive there, it is necessary to adjust itself to some type or types of habitat to which it must fit itself accurately. Thus it is a commonplace in such circumstances to find that species normally of wide tolerance exist only in specialized habitats. Alternatively, or in addition, those which show little variability, whether in the strict sense of that term or in respect of a given form of continuous variation, may at the edge of their range split up into groups each with its own marked characteristics. The localities which they inhabit may in fact differ from one another ecologically and in climate to an extent which is small compared with that encountered within the normal range of the species, but at the fringe of its distribution it is only by close adaptations to them that it can survive.

As Darwin himself so clearly realized, such local races are unable to evolve without some type of isolation. To-day we should extend this term to include a cline, which to provide an isolating mechanism must be long compared with the capacity of the species for movement. But the whole situation tends in fact to favour geographical isolation, through the survival of the population only in pockets where the conditions are relatively favourable to it. From these it may later spread if it adjusts itself successfully to them.

As Darlington (2) points out, another means of isolation at the edge of a species' range is the cytological one. Thus great numbers of plants, and doubtless some animals, prove to be polyploids in such situations. They are then free to adapt themselves without the difficulties introduced by constant crossing with the main bulk of the species behind them, as it were. Moreover, geographical isolation may allow a sufficient reconstruction of chromosome material to give genetic isolation without polyploidy when, owing to subsequent expansion as a result of successful adaptation, different groups meet. The formation of chromosome-loops during meiosis in the hybrid specimens will be a strong indication that this type of isolation had been successfully achieved.

In the peculiar conditions at the edge of a species' range, selection for new and appropriate habits may be of much importance. Thus the butterfly *Papilio machaon*, found over a large part of central and southern Europe and elsewhere, has an extremely wide environmental tolerance, occurring from sea level to a considerable height in the Alps, and inhabiting marshes, dry plateaux and other types of situation. In England it reaches the limit of its range and is established only in a few places, in Cambridgeshire and East Anglia, where it is entirely restricted to fens. Here the individuals, though powerful on the wing, are very localized, though normally they scatter widely over the countryside: an exceptional adaptation of obvious importance to a population adjusted to a single and restricted type of habitat.

One of the great opportunities for the study of evolution in wild populations is provided by the marked fluctuations in numbers to which so many species are subject. There have been attempts, apparently successful in respect of some rodents, to associate these with general climatic changes depending, for instance, upon sun-spot cycle, and to show therefore that they affect populations synchronously over vast areas. But this is a special aspect of a far more general phenomenon ; for plant and animal communities automatically generate their own fluctuations in numbers which therefore often occur independently in different localities. Moreover, such changes in density increase enormously the rate of evolution especially in isolated colonies. They arise in the following way.

When an animal or plant increases in numbers in some locality it does so because variations in environment chance temporarily to favour it there. That is to say, some aspects of selection are then relaxed. Therefore genes and genic arrangements which would normally be eliminated can survive and can be tried out in new combinations, some of which may prove of advantage to the organism. But when conditions change again and become more rigorous the population will be particularly unfitted to withstand them owing to the relatively unsatisfactory genotypes which have spread in it. Thus numerical increase with marked variability inevitably prepares the way for numerical decline with stricter elimination and reduced diversity. But the opportunities for assessing genes in new combinations which thus arise might take a very large number of generations to achieve in a numerically stable community.

I had already reached these conclusions forty years ago when I began work upon a colony of the butterfly *Melitaea aurinia*. However, they were not published until 1930 (17), since that species has but one generation in the year and it was necessary to study it in various phases of its cycle. Thus the work required to substantiate such views by means of a concrete instance involved long delay.

These results have often been reviewed (16), so that they can be restated very briefly now. An examination of records kept by collectors in the past, combined with our own observations, showed that the species was abundant in the locality we studied from 1881–97, after which it declined to small numbers and became very rare from 1912–20. During the whole of this time the specimens were remarkably constant in appearance. From 1920–24 the colony underwent a spectacular numerical increase associated with a great outburst of variability; hardly two individuals were alike while many of the more unusual varieties were deformed. From 1925–35 the increase in numbers ceased and the butterflies became relatively constant once more, but the form which then predominated differed from the one which characterized the population before 1920. That is to say, an opportunity for rapid evolutionary change had occurred and the insect had made use of it. Unfortunately precise numerical estimates, which would have been desirable throughout the whole period, could not then be made since the methods for obtaining them, by means by marking, release and recapture (8, 13) had not at that date been devised. It is a depressing fact that though corresponding phenomena are constantly being reported, little detailed work along these lines has been undertaken subsequently. Another colony of the butterfly is, however, being studied from this point of view at the present time.

When during a period of rapid increase recombination brings together major genes which chance to interact in an advantageous way, selection will favour the evolution of close linkage between them. This may be continued to the point when they act approximately as a single unit and become super-genes. Thus to an increasing degree the organism will tend to have the advantage of their combined effects. These can then be improved through adjustment of the gene-complex, especially if some of the more important genes enhancing their actions can be transmitted with them in a block, for example in an inversion.

It will be noticed that such repeated fluctuations in numbers with their great evolutionary potentialities will override and obscure the effects of the " founder " concept to which attention has already been drawn (p. 42). Moreover, the uniformity of the environment in Dobzhansky's cages, set up to demonsrate that principle, prevented marked numerical fluctuations in his experimental populations and thereby produced an entirely unreal situation, as did the exclusion of such fundamental ecological distinctions as face populations inhabiting small and large natural habitats respectively.

Indeed the periodical reduction to small numbers occurring in populations in general may occasionally produce something like a repetition of the " founder " situation when taking place in isolated communities inhabiting small areas. But evidently its evolutionary importance lies not in the particular genes carried by the survivors but in the release of variability which occurs when the numbers expand, together with the application of stricter selection as they contract once more. Moreover, the reduction to a level so low as to resemble the initial population envisaged in the founder concept is probably unusual and extreme. However, the evolutionary effects of fluctuation in numbers as outlined here will occur whatever may be the minimum attained : for it is the relatively large numerical change that is important, not the size of the colony reached at the lowest point of a cycle.

The most fruitful means of studying evolution in natural populations has been reserved to the last : it is that provided by polymorphism. This condition is one in which major genes, or super-genes, and their allelomorphs possess selective advantages balanced, except where the condition had not yet achieved stability, by disadvantages. Thus even their rarer phase must be substantially too frequent to be maintained merely by mutation. The opportunities for the evolution of the characters which they control are therefore great, while such a situation is itself the outcome of selective adjustment of an accurate, because balanced, kind.

The precise definition of polymorphism was supplied by Ford in 1940 (10) and it is now sufficiently well known to require no restatement in an article on evolution or genetics. It is necessary only to remark that the condition excludes seasonal, geographical and continuous variation, as well as rare disadvantageous qualities. Nor is there any need to retrace the arguments already often elaborated (15) to demonstrate that the genes concerned cannot be selectively neutral.

Since a polymorphism involves discontinuous variation within a population, its phases must be controlled by some switch mechanism, which is nearly always genetic. This will generally result in the superiority of the heterozygote even in those situations which tend automatically to promote diversity, such as Batesian mimicry, because the advantageous effects of the switch gene (or super-gene) will become dominant while its disadvantageous ones will become recessive. Therefore the heterozygote will manifest advantages only, while both homozygotes will give rise to some advantageous and some disadvantageous qualities.

The ecological necessity for a polymorphism is often apparent, but the advantages of the heterozygote are generally of a physiological kind the nature of which may be elusive though their existence can be proved. A few of the well known instances in which polymorphism has served to demonstrate evolution in process, or its recent results, may be cited to illustrate these considerations and slightly to extend them.

It may first be observed that the significance of a polymorphism may be quite obscure. For example, the moth *Panaxia dominula* (Hypsidae) is polymorphic in an isolated locality at Cothill fives miles from Oxford. Three forms are involved, controlled by a single pair of allelomorphs with the three genotypes all visibly distinct. The species has but one generation in the year, and in this locality it has been studied since 1939. The rarer allelomorph of the switch gene concerned has varied irregularly from 11·1 to 1·1 per cent. of available loci in a season, the maximum and mimimum occurring respectively in 1940 and 1955; for the last two years the gene-frequency has been rising. From 1941 the size of the population has been assessed by the marking, release and recapture of specimens. Now under Mendelian inheritance it is possible to determine whether or not changes in gene-frequency can be the result of random genetic drift provided they, and the size of the population in which they occur, can be calculated (7). Such data are available in this instance and they demonstrate that the observed fluctuations in gene-frequency cannot be due to chance but must be the result of selection varying in intensity and direction from one year to another.

When these results were first published (8) they were criticized by Sewell Wright (28). The accumulating data of subsequent years made it possible to refute each of his objections in a way which he appears to have found unanswerable (24), and indeed the control of this diversity in *Panaxia dominula* as a balanced polymorphism is not now in doubt. It involves differences in colour and pattern, also in mating habits (25). The latter effect is a curious one, since the female prefers to pair with a male belonging to any other genotype than her own: a situation which, favouring as it does the rarer forms, tends to maintain the polymorphism, though it is certainly not alone responsible for doing so.

The work of Cain & Sheppard upon the polymorphism of the snail *Cepaea nemoralis*, on the other hand, demonstrates selection favouring characters of obvious survival value (1). They find that there is a heavy excess of yellow shells (greenish when the living animal is within) on a green background such as downland, and of brown shells upon a dark one such as the floor of a beech wood. Also that there is an excess of banded shells in diversified conditions, such as a mixed hedgerow, and of plain upon a uniform one. An important predator of this snail is the Song Thrush, *Turdus philomelos*[1], which carries it to favourite stones upon which it breaks open the shells. At such places the broken fragments accumulate, so that by comparison it is possible to determine whether or not the elimination carried out by the birds is a random one. In fact, in each type of locality they remove a heavy excess of the inappropriate coloured and marked specimens. Moreover, in spring as the countryside and woods become greener the selective advantage of the different types alters (23). This is one reason why the population does not reach uniformity in different habitats; another is the opportunity for rapid adjustment to changing conditions which the diversity confers.

The polymorphism is, of course, controlled by major genes: yellow shells are recessive to the darker shades (pink and brown), and the possession of bands is recessive to their absence. There is, as might be expected, linkage between the two loci concerned, and there is accumulating evidence that the cross-over value between them varies in different populations. This matter is under investigation. It suggests that we here see the evolution of linkage which, to different degrees in different habitats, holds together those allelomorphs which produce the type of colour and banding that is most advantageous there.

That the selective advantage of a polymorphism can be attained by distinct means in different regions is a natural deduction from the great opportunities for micro-evolution offered by this situation. Thus the moth *Triphaena comes*, Agrotidae, is polymorphic, with light and dark forms, in the Outer Hebrides, Orkneys and some parts of the Scottish mainland. Further south only the light form occurs. The dark phase is an incomplete dominant, the homozygotes being on the average darker than the heterozygotes but overlapping them. It has been shown that in the Outer Hebrides and in Orkney the same major gene acts as a switch controlling the two forms but that dominance has been independently acquired by the accumulation of different sets of modifiers (14). In this work, no clear excess of heterozygotes above expectation was detected, though the numerical values of several of the broods were exceptional. It must be remembered, however, that a single female lays three hundred eggs or so, while in a state of nature perhaps only four or five of her progeny reach the moth state. In breeding experiments, the survival rate is on the average greatly improved : in many of the families raised during the course of this work several dozen, and in some over one hundred, individuals survived to become imagines. That it to say, selection was very greatly mitigated, so that relative differences in the survival of genotypes which might be extremely important in the wild can be obscured in the laboratory.

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[1] Syn. *T. ericetorum.*

This was demonstrated experimentally in 1940 during the course of genetic work on the moth *Boarmia repandata*, (Selidosemidae) (9). In stocks raised in the laboratory, there proved to be a slight but negligible excess of " melanics " compared with the normal form in segregating families : a distinction which became clearly significant when the elimination was increased by partial starvation. This was the first time that a physiological difference favouring the heterozygous black specimens had been demonstrated in respect of industrial melanism.

That phenomenon is of the highest importance since it represents the most striking evolutionary change ever actually witnessed in any organism, animal or plant. In recent years it has been analysed with outstanding success by Kettlewell using a combination of genetic work in the laboratory and observation in the field (18, 19, 20).

Black forms of more than sixty species of moths have been, or are, spreading in the industrial areas of Britain and replacing those normally coloured. A similar change is occurring in continental Europe and the U.S.A. though it has not yet been subjected to detailed analysis there. All the species concerned rest fully exposed on tree trunks, rocks or fences, where they derive protection from resemblance to bark or lichen. The melanic forms are, however, at an advantage in the blackened countryside of manufacturing districts, presupposing that the resting moths are preyed upon by birds. This, however, both ornithologists and entomologists were until lately unwilling to grant. The work of Kettlewell has proved them wrong. He has demonstrated that such moths are when at rest selectively eliminated by birds in great numbers, and has shown why that fact has not heretofore been recognized : for the act of predation is so rapid that it requires large-scale experimental work and observation to detect it. Moreover, where the black forms are the better concealed, they are in addition free to exploit their physiological advantages, accumulating in the heterozygote, which are particularly valuable to them when feeding upon polluted vegetation.

Working upon the Peppered Moth, *Biston betularia*, Kettlewell has shown that the melanic form spreads eastwards across England from manufacturing districts far into rural areas, a fact which has demonstrated the unexpectedly great drift of pollution with the prevailing westerly winds. He has also established that the black phase has *evolved* ; it is now detectably more extreme than when it first began to increase a hundred years ago. This important observation he is testing by crossing the black insects with specimens from parts of the country where only the pale form is known. By repeating the process in their progeny for several generations he is introducing the gene for melanism into a gene-complex which has had no experience of it.

Industrial melanism provides one of the rare instances in which it is possible to study the development of a polymorphism from its inception. Owing to the evolution of heterozygous advantage, it is unlikely that the black forms will spread even in manufacturing districts until they reduce the pale ones to the status of a rare mutant. In *Biston betularia*, there is an indication in some localities that the melanics may become stabilized at about 98 per cent. of the population, at which level the gene responsible for them would occupy 85·9 per cent. of available loci if all three genotypes were equally viable. Their heterozygous advantage will, in fact, reduce it somewhat below that value.

The properties of a polymorphism, which ensure that the various phases cannot be of neutral survival value, but will be maintained by contending advantages and disadvantages, of course apply wherever that condition is found. Therefore they do so to Man, one of the most polymorphic of animals ; a fact the profound implications of which would have particularly interested Darwin.

The blood groups were first treated as an example of polymorphism in 1942 (11). A logical deduction from that concept led to the prediction in 1945 (12) that members of the different blood groups would not be equally susceptible to specific diseases. That conclusion received concrete support six years later when evidence was obtained that infants dying of broncho-pneumonia during the first two years of life belong disproportionately often to blood group A of the OAB Series (26). Other and fully established instances demonstrating the association between human polymorphism and particular diseases are now accumulating in a way which is opening up a new branch of medicine (22). Thus the study of evolution is contributing not only to natural knowledge, which is its primary purpose, but also to human welfare.

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CHEMICAL EVOLUTION IN PLANTS

By R. DARNLEY GIBBS
(*McGill University.*)

(With 3 Text-figures.)

Some thirteen years *before* the 1858 meeting of The Linnean Society of London at which Charles Darwin and Alfred Russel Wallace presented their memorable papers, John Lindley's *Vegetable Kingdom* appeared. In the preface he tells us that he was urged :

> " . . . to introduce among the properties of plants an account of their proximate principles and ultimate constituents. But after a full consideration of the subject, he has come to the conclusion that it is not expedient to do so. In the first place, such matters belong to Chemistry, and not to Botany ; secondly, it does not appear possible to connect them with any known principle of botanical classification ; and, moreover, the extremely unsteady condition of the opinions of chemists themselves upon the results of their own researches, would render the introduction of the supposed results of chemists embarrassing rather than advantageous."

Lindley then used the apparently sporadic occurrence of one or two constituents in plants as a further argument against the use of chemistry as an aid to classification. Nevertheless he was constrained at times to mention the chemical properties of groups of plants. Thus we find on p. 614 of the third edition of his book (1853) this paragraph about the Gentianaceae :

> " The Order [family] of Gentianworts is not more remarkable for the diversity of its colours than it is for the uniformity of the secretions which its various species exhibit. Bitterness in every part, root, leaves, flowers, fruit, in annuals, perennials, and shrubs, is so much their characteristic that the following account of the purposes to which they are applied is little more than a list of repetitions ; with this exception, that they in some cases prove narcotic and emetic."

Some twenty-eight years *after* the Darwin-Wallace papers appeared we find a remarkable woman—Helen C. de S. Abbott—publishing a paper entitled " Certain chemical constituents of plants considered in relation to their morphology and evolution." In it she says :

> " The facts obtained from these studies tend to show a chemical progression in plants, and a mutual dependence between chemical constituents and change of vegetable form. . . . The evolution of chemical constituents in which they follow parallel lines with the evolutionary course of plant forms, the one being intimately connected with the other, and consequently that chemical constituents are indicative of the height of the scale of progression, and are essentially appropriate for a basis of botanical classification. In other words, that the theory of evolution in plant life is best illustrated by the chemical constituents of vegetable form."

In the following year she writes :

> " The vegetable kingdom does not usually claim our attention for its intellectual attainments, although its members would certainly seem to possess greater chemical skill than a higher race of beings exhibit in laboratories."

and (in another paper in the same year) :

> " There has been comparatively little study of the chemical principles of plants from a purely botanical view. It promises to become a new field of research."

In 1888 Greshoff was assigned to the great botanical garden at Buitenzorg (Bogor) in Java to institute a chemico-pharmacological investigation of the plants of what was then the Dutch East Indies. He returned to Holland in 1892 and continued his researches there. Later he worked at Kew and recorded the results of his studies in a paper which appeared in 1909. Here we read :

> " Since plants are no longer classified according to a single character (i.e. according to an artificial system), but attempts are made to unite into natural groups such plants as are considered to be related, the systematic botanist desires to know that relationship in *all* its manifestations."

He defines "' Comparative phytochemistry " as " the knowledge of the connection between the natural relationship of plants and their chemical composition." He notes that there are whole families of plants of which we know nothing chemically, and goes on to say that :

> " Strictly speaking one might demand that every accurate description of a new genus or of a new species should be accompanied by a short 'chemical description ' of the plant."

It is evident that there was growing up a belief that if plants are related to one another as the views of Darwin and Wallace would suggest, then their chemistry should reflect these relationships ; nearly-related plants being more alike in their chemical make-up than distantly-related ones. It is but a step further to argue that a " primitive" plant will be chemically primitive and an " advanced " one chemically advanced. This was assumed to be the case by such men as Baker & Smith in Australia.

Smith was associated for a while with Maiden and started with him his work on the Eucalypts. In 1899 he and Baker came together and worked as a remarkable team until their retirement in 1921. They published in 1902 " A research on the Eucalypts, especially in regard to their essential oils." In this they summarized work on the botany and chemistry of more than 100 species of *Eucalyptus* L'Hérit. They concluded that the genus has evolved from *Angophora* Cav. and that new species have arisen as it has spread through Australia and Tasmania from the north-west to the south-east. They were able to arrange the species studied in groups which differ both morphologically and chemically. The more primitive species have feather-veined leaves and much pinene in their essential oils ; more advanced ones have intermediate venation and oils with pinene and cineole ; still more recent species have butterfly-wing venation and oils with phellandrene, and piperitone or geranyl acetate. We have reproduced their chart of relationships in modified form (fig. 1).

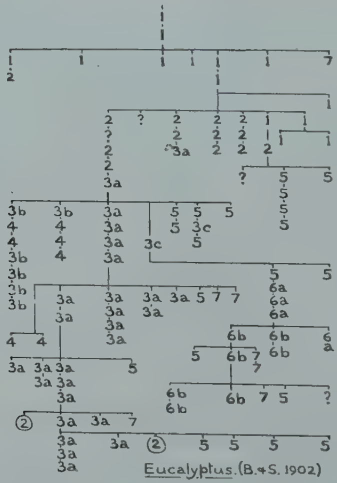

FIG. 1.—Relationships within the genus *Eucalyptus*. The numbers indicate the groups to which Baker & Smith assigned the species in 1902. Compare with Table I.

In 1920 the second edition of their " Research " appeared. This contains information on no less than 176 species of *Eucalyptus* which are arranged in groups differing slightly from those of the first edition. We give, in Table I, a summary of the groupings from the two editions.

TABLE I.—Classification of Eucalypts (Baker & Smith, 1902 and 1920).

1902		1920	
Group. Species	Composition of oils	Group. Species	Composition of oils
I 1–14	Largely pinene. Little or no cineole.[*] No phellandrene.	I 1–21	Largely pinene. Little or no cineole. No phellandrene.
II 15–29	Pinene. $< 40\%$ cineole. No phellandrene.	II 22–46	Pinene. $< 40\%$ cineole. No phellandrene. No aromadendral[†].
III*a* 30–56	Pinene. $> 40\%$ cineole. No phellandrene.	III*a* 47–70	Pinene. 40–55% cineole. No phellandene. Aromadendral rare.
III*b* 57–62	Pinene less. $> 40\%$ cineole. No phellandrene. Aromadendral appearing.	III*b* 71–91	Pinene. $> 55\%$ cineole. No phellandrene. No aromadendral.
III*c* 63–64	$> 40\%$ cineole. Phellandrene appearing.		
IV 65–71	Pinene. $< 30\%$ cineole. No phellandrene. Aromadendral present.	IV*a* 92–101	Pinene less. $> 40\%$ cineole. No phellandrene. Aromadendral appearing.
		IV*b* 102–106	$> 40\%$ cineole. Phellandrene appearing.
V 72–91	Pinene. $< 30\%$ cineole. Phellandrene present.	V 107–124	Pinene. $< 40\%$ cineole. Usually no phellandrene. Aromadendral present.
VI*a* 92–95	$< 30\%$ cineole. Phellandrene present. Piperitone[‡] present.	VI 125–148	Pinene. $< 40\%$ cineole. Phellandrene present.
VI*b* 96–102	Little or no cineole. Phellandrene present. Piperitone present.		
VII 103–109	Oils not readily placed.	VII*a* 149–155	40% cineole. Phellandrene present. Piperitone present.
		VII*b* 156–166	Little or no cineole. Phellandrene present. Piperitone present.
		VIII 167–176	Oils not readily placed. Little or no cineole.

[*] Called " Eucalyptol " in 1902.
[†] A name used for the mixture of aldehydes (cuminaldehyde, cryptal, etc.).
[‡] Called " Peppermint ketone " in 1902.

Read (1944) gives an interesting survey of this work. Penfold & Morrison, in the fourth volume (1950) of Guenther's treatise on the essential oils, are somewhat critical of the claims of Baker & Smith, their own researches having revealed more variation in chemistry than those authors found. We must remember, however, that we have, in the work of Baker & Smith, a remarkable pioneer effort to study chemical as well as morphological evolution and to relate the two. There are all too few researches of this nature even to-day.

What Baker & Smith tried to do for a genus, McNair tried to do for the plant kingdom, and with less success, as might be expected. Between 1929 and 1945 he produced a series of papers dealing with plant chemistry and systematics. In 1935, for example, he writes on " Angiosperm phylogeny on a chemical basis ". Here he assembles data on molecular weights of alkaloids, on iodine numbers (as measures of unsaturation of fats), and so on. His criteria are that the most highly evolved alkaloids have the highest molecular weights (i.e. are most complicated ?) ; that the most highly evolved fats have the highest iodine numbers (i.e. are most unsaturated); and that the most highly evolved volatile oils have the highest specific gravities and the lowest refractive indices. A sample table, from which it is concluded that the family Magnoliaceae is the most primitive of the families being considered, is reproduced here (Table II).

TABLE II.

Family	Dominant form	Alkaloids (mol. wts.)	Fats (iodine Nos.)
Magnoliaceae	Tree-shrub	—	95·5
Lardizabalaceae	Shrub	—	78·4
Berberidaceae	Shrub-herb	330	139·1
Ranunculaceae	Herb	543	145·0

It is doubtful if McNair's assumptions are justified. Manske, whose opinions upon alkaloids should carry great weight, writes :

> " The type of alkaloid in a plant, that is, its complexity judged by the number of carbon and nitrogen atoms, is *not* a criterion of the stage of evolution."[1]

In a paper which appeared in 1945 McNair deals with " Some comparisons of chemical ontogeny with chemical phylogeny in vascular plants ". Here he discusses the principle of recapitulation and concludes that in seeds there has been a series from those with carbohydrate to those with saturated oils and then to those with unsaturated oils. The idea that Monocotyledons are more primitive than " Archichlamydeae " and these more primitive than " Sympetalae " is supported, he says, by such chemical evidence as that summarized in Table III. We may greet this conclusion with some scepticism.

TABLE III.

Groups	Embryos		Albumen		General contents
	% Starchy	% Oily	% Starchy	% Oily	% Oily
Monocots.	12	45	57	27	15
Archichlam.	15	45	16	30	50
Sympet.	9	42	2	40	54

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[1] Personal communication, 28 October, 1957.

In the same paper he deals with the occurrence of cyanogenetic glycosides in plants. He writes that they :

> " . . . occur more generally in the more advanced of the older groups and also in the more advanced families of the different orders . . . In the Archichlamydeae of the dicotyledons cyanogenetic glycosides have not been found in the first eleven orders (which consist mostly of woody plants).[2] They have been found in nearly all of the remaining 19 orders. .. . As to the occurrence of cyanogenetic glycosides in the more advanced families of the various orders the following examples may be considered as indicative. In the Rosales the substances mentioned are found in the 4. Crassulaceae, 6. Saxifragaceae, 14. Platanaceae, 16. Rosaceae, and 18. Leguminosae. In the Parietales the containing families are 17. Winteranaceae (Canellaceae), 19. Flacourtiaceae, and 23. Passifloraceae. In the Myrtiflorae the producing families are : 9. Lecythidaceae, 14. Myrtaceae, 15. Melastomaceae, 16. Onagraceae, and 17, Haloragidaceae."

Now McNair apparently used the arrangement and numbering of Engler's " Syllabus ", edition 7 (see key at the end of Willis, 1955). The " first eleven orders " referred to are now regarded as advanced and reduced rather than as primitive. In Benson (1957), for example, they are numbered 56, 19, 47, 53, 51, 50, 48, 55, 49, 54, and 52 ; and the HCN-producing orders have a " below average " numerical placing. As to the occurrence of cyanogenetic glycosides in the Rosales, the position of the families having these glycosides is only a little "above average " (treating the order as a linear series of families, as McNair seems to have done). If McNair had used the 11th edition of Engler's " Syllabus ", which appeared nine years before his paper, the occurrence would have seemed even nearer to average.

His reference to HCN in the Parietales is of great interest to the writer. Cyanogenetic glycosides occur not only in the families mentioned by McNair—Winteranaceae (Canellaceae), Flacourtiaceae, and Passifloraceae—but also in the Turneraceae.[3] Now these families to not constitute families 17, 19, 21, and 23 (using the numbering of " Syllabus " edition 7) of a linear series, *but they are all members of a suborder Flacourtiineae*, as Engler makes clear in edition 2 of *Die natürlichen Pflanzenfamilien* (vol. 21, p 5, 1925). They are also exactly the order Violales of Benson (1957). That is, they are closely related. We have summarized the occurrence in them of cyanogenetic glycosides in Table IV. It will be seen that we have no informa-

TABLE IV.—Occurrence of cyanogenetic glycosides in the sub-order Flacourtiineae of the Parietales.

Family	Genera/Species	HCN		
		Present	Doubtful	Absent
Canellaceae	5/11	1/1	—	—
Violaceae	16/850	—	1/2	5/20*
Flacourtiaceae	84/850	9/17	2/2	9/10†
Stachyuraceae	1/5–6	—	—	—
Turneraceae	7/110	3/11	—	2/3‡
Malesherbiaceae	1–2/35	—	—	—
Passifloraceae	11/600	3/31	—	1/1‡
Achariaceae	3/3–4	—	—	—

* From herbarium material in 1/5.
† „ „ „ „ 4/4.
‡ „ „ „

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[2] Henry (1906) says they have been reported from Salicaceae (order 3). I have no other record of this.

[3] Gibbs (unpublished data).

tion on 3 of the 8 families involved, and that only a small proportion of the genera and species of the other families have been investigated : a state of affairs typical of our knowledge of comparative plant chemistry.

The Violaceae may well be out-of-place here. Copeland (1957) places them in the Rhoeadeae (Rhoeadales), while Hallier (1912) puts them in the Polygalinae (Polygalales). If the Violaceae do belong in the Flacourtiineae we might argue that they have lost or are losing the power to synthesize cyanogenetic glycosides. Camp (in Gundersen, 1950) argues that the family is primitively a woody one, which arose in South America and gave rise to our herbaceous northern violets. It would be interesting to know if HCN can be found in the most primitive surviving woody members in South America.

While we may not be able to decide whether the occurrence of *HCN* in the Parietales is advanced or no, we may well conclude that the occurrence in this order of *raphides* (one of the few directly-visible chemicals) is a primitive character. They are found in Dilleniaceae (where they are sometimes small and unarranged), in Actinidiaceae (except *Sladenia* Kurz.), in Marcgraviaceae, and in Theaceae, all members of Engler's first suborder—Theineae. The Dilleniaceae are certainly primitive (see discussion in Gibbs, 1954, pp. 26–28), as are the Actinidiaceae. *Sladenia*, which does not contain raphides, should, perhaps, be placed in the Theaceae. The Marcgraviaceae are closely related to the Theaceae, says Engler.

The Theaceae do not for the most part contain raphides. They have been observed there only in *Tetramerista* Miq., *Pelliciera* Planch. & Triana, and *Trematanthera* F. Muell., all of which may be removed from the family. The first two have sometimes been placed in the Marcgraviaceae (where raphides *do* occur, see above), while *Trematanthera* has sometimes been included in the genus *Saurauia* Willd. of the Actinidiaceae, which contains raphides.

These " primitive " raphide-forming families of the Parietales have evolved, we suppose, from woody members of the Ranales (in the Englerian sense). The latter order (in the 11th syllabus of Engler & Diels) has nineteen families in four suborders. The first seven families do not, so far as we know, contain raphides. The eighth—Menispermaceae—is said by Santos (1931) to have two genera which produce them, *Anamirta* Colebr. and *Archangelisia* Becc. A study of Santos' drawings, however, show needle-crystals but not true raphides in the tissues of these plants. The following six families also seem to lack raphide-forming members. The fifteenth—Myristicaceae—forms acicular crystals but not true raphides. The sixteenth—Gomortegaceae—forms needle-like crystals. The next family—Monimiaceae—is said by Metcalfe & Chalk (1950) to form raphides " . . . often in special cells in the unlignified tissues". These would seem to be true raphides.[4] In the family Lauraceae, which is placed next, acicular crystals are found, and Santos (1930) has reported " raphides " in two species of *Cinnamomum* L. His drawing (Pl. 6, fig. 24) of a cell from *C. cassia* Bl. certainly shows needle-crystals in more or less parallel bundles, but the cell is hardly a typical raphide-sac. In the last family—Hernandiaceae—acicular crystals, and perhaps also raphides, are said to occur.

If we consider Hutchinson's (1926) arrangement of the families mentioned above we find that, with the exception of the Menispermaceae at the " top " of the Ranales-Berberidales " tree ", the families which have anything approaching raphides all lie in his *Laurales* (fig. 2). Is it from this group that the Dilleniaceae, etc. arose ?

The chemistry of the monocotyledons is not very different from that of the dicotyledons. This would seem to support the view that one group has arisen from the other, or that they have a common ancestry. One view is that the monocotyledon. arose from primitive dicotyledons such as the herbaceous members of the Ranaless

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[4] Metcalfe (letter of 17 December, 1957) says " Raphides were actually observed at Kew in *Doryphora sassafras* Endl., *Peumus boldus* Molina and *Laurelia novae-zeylandiae* A. Cunn. Judging from Solereder's remarks, however, raphides appear to occur generally in the Monimiaceae".

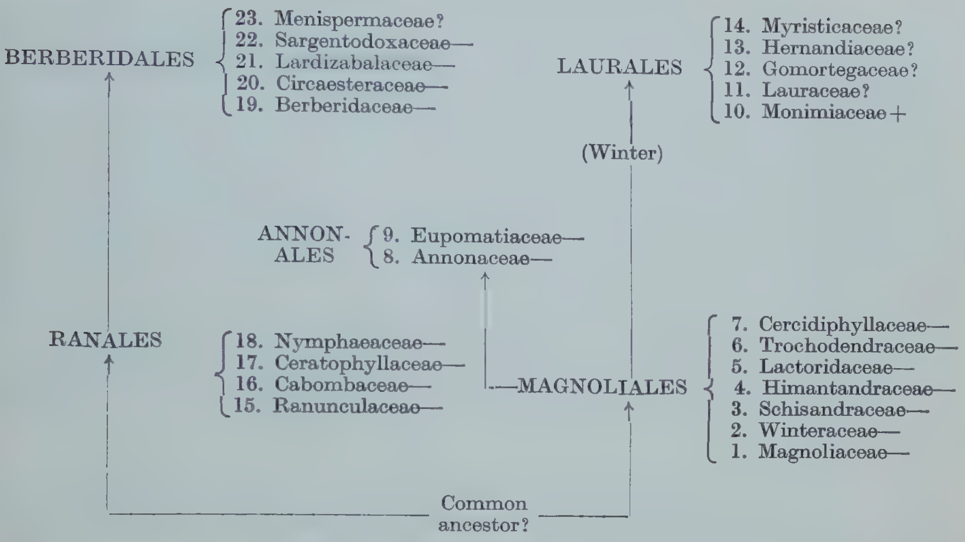

FIG. 2.—Essentially the families of the Ranales of Engler & Diels as arranged by Hutchinson. Families which seem to be without acicular crystals and "raphides" are marked (—); those with acicular crystals and/or "raphides" are marked (?); those known to have true raphides are marked (+).

Now we have seen above that these do not have raphides: and neither do the primitive monocotyledons. Kimura (1956) has published one of the most recent "arrangements" of the whole group of monocotyledons. He would have the Alismatales (1) arising from proto-Polycarpicae (proto-Ranales) and giving rise to Hydrocharitales (2) and Scheuchzeriales (3). From the proto-Scheuchzeriales he would derive Triuridales (6) and Potamogetonales (4), and from the proto-Potamogetonales he would derive the Najadales (5). Now raphides seem to be absent from all these groups, though our knowledge of them is far from complete. They *do* occur, however, in the Liliales (7) and in many other orders of the monocotyledons. If Kimura's arrangement (fig. 3) is correct then raphides arose independently in the monocotyledons after they

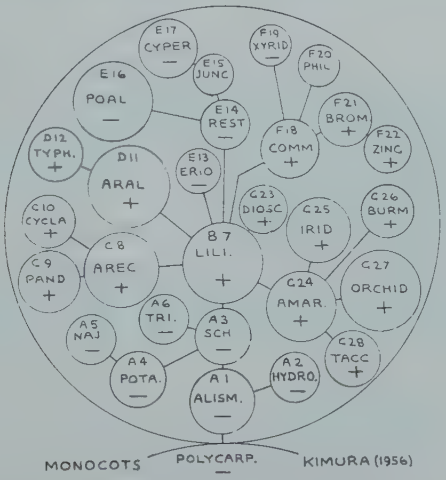

FIG. 3.—Kimura's arrangement of the orders of Monocotyledons. Orders known to contain raphide-producing species are marked (+); those believed to lack them (—).

had diverged from the dicotyledons—an example of parallel evolution. They arose only once in this group, it would seem, and dropped out in at least one branch (Kimura's Sicciflorae fig. 3, E 13–17). In the dicotyledons they must have arisen several times, for they occur not only in the families mentioned above, but in several other groups. They are found, for example, in *Greyia* Hook. & Harv. of the Melianthaceae (or Greyiaceae), the only occurrence in the family, and in the Balsaminaceae (*Impatiens* Riv. ex L. and *Hydrocera* Bl.). Both of these families are placed in the Sapindales, where raphides seem otherwise to be absent. They do not occur in *Trapa* L., but are present in the Oenotheraceae (see Gibbs, 1954, pp. 4–5 and 17); in several families of the Centrospermae; and in the subfamily Rubioideae of the Rubiaceae (Bremecamp, 1952).

It would not be just to leave this discussion of the occurrence of raphides in the flowering plants without a tribute to the pioneer work of Gulliver, who published, in 1866, a paper " On raphides as natural elements in the British flora ". In this paper he records their distribution in considerable detail, and says that it may be of use in taxonomy. Further, and importantly, he stresses the constancy as a character of these crystals :

> " In short, I know of no means by which a raphidean plant can be grown in health, if at all, so as to extinguish this character, nor by which a plant regularly devoid of raphides can be made to produce them."

In this article I have tried to show some of the biochemical lines along which our taxonomic thinking has developed in the hundred years that have passed since Darwin and Wallace electrified the scientists (and others) of the nineteenth century. Organic evolution, and with it biochemical evolution, are now generally accepted as facts, but we know all too little of the biochemical facts. At least one book (Florkin, 1949) has appeared with the title *Biochemical Evolution.* Its translator (Morgulis) points out that " It is, of course, unfortunate that the factual material is drawn entirely from the animal kingdom ". We may consider it unfortunate that this was not indicated in its title !

The development of modern methods—such as those of chromatography—make it ever easier to investigate the chemistry of living organisms. We may be confident that the coming century will see the publication of books on the biochemical evolution of plants that will be based upon incomparably better evidence than is available to us in 1958.

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HABITS OF LIFE AND EVOLUTION OF BODY DESIGN IN ARTHROPODA

By S. M. Manton, F.R.S. (Mrs. J. P. Harding).
(Zoology Department, King's College London and the British Musuem (Natural History).)

(With Plates 1 & 2 and 1 text-figure.)

Introduction.

Within many animal phyla species exist which show detailed structural adaptations to particular environmental circumstances. The hermit crabs are time-honoured examples. The diagnostic characters of many classes and orders have on the contrary been regarded largely as non-adaptive in respect of habitat, and systematists have valued so-called non-adaptive features as useful bases for classification. In recent years the study of living Arthropoda has demonstrated the functional significance of a large number of diagnostic characteristics of classes and orders which hitherto have held no more than classificatory significance for us. Correlations between the sensory and feeding equipment of the head and habits of arthropods have been appreciated for many years, but it is now clear the trunk features also are associated in great detail with habits of life (see Parts 1–6 and future parts)[1].

Habits of Life of Evolutionary Significance.

Animals living in the same environments may possess very different habits. For example, the Onychophora, Pauropoda, Symphyla, Chilopoda, Diplopoda (Pls. 1 and 2), scorpions and many hexapodous arthropods may live in or under the same decaying log, but the habits of these animals are significantly different. This differentiation of habit, and the morphological features which accompany each habit, must have evolved together. Structural advances of this nature enable animals to live better in a wide variety of circumstances, in contrast to the detailed specializations of the hermit crabs and other animals which have perfected their abilities to live in one particular niche.

Habits of life which appear to have been of evolutionary significance vary greatly in their ease of recognition because they may not be exercised all the time. A centipede (Chilopoda) (Pl. 1, figs. 6, 7, and Pl. 2, fig. 9) and an ungulate both show their maximum speeds with reluctance because slower movements can be accomplished with greater mechanical efficiency and are therefore preferred. But it is the ability to run fast occasionally, and perhaps at great cost, which results in escape from a predator or the catching of prey, and it is these accomplishments which have determined the pattern of skeleto-muscular evolution, and not the leisurely movements more frequently employed. However, animals whose basic construction is largely associated with speedy running are usually easy to recognize.

Habits of evolutionary significance which are less easy to recognize may be exemplified by those of *Polyxenus*. This sucker-footed millipede (diplopod), alone among Myriapoda, can live upside down on a glass-smooth surface, making temporary excursions elsewhere for feeding. When predators and climatic conditions allow, *Polyxenus* spreads into a wide variety of habitats ranging from crevices under bark to the leaves of trees, among the branches of coastal plants, some inches into soil, and deep into old stone walls or among rocks. When conditions become rigorous, then the special proficiencies of the animal for living on ceilings of narrow-mouthed crevices, where less sure footed predators cannot follow, may determine survival, together with the several structural devices and habits which result in escape from enemies, floods and drought (Part 5). Abundant cast skins stuck to smooth rock ceilings, together with animals of all ages, can be found some distance from vegetable food upon which *Polyxenus* depends.

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[1] The series of papers on the evolution of arthropodan locomotory mechanisms, and other habits of life (Manton, 1950–58) which have already appeared in the *J. Linn. Soc.* (*Zool.*), or are in course of preparation, are referred to as Parts 1–8 on the following pages.

Burrowing may be an alternative occupation to surface running for many creatures, and has often played a large part in shaping their bodies. Geophilomorph centipedes (Pl. 1, figs. 3–5) have adopted the earthworm-like method of utilizing the body muscles to provide the burrowing force when the segments thicken and widen, while a bulldozer-like technique using armour plating and the force of the limbs is employed by millipedes (Diplopoda) (Pl. 1, fig. 2). All the conspicuous trunk features, entirely different in these two groups, are correlated with this habit. In the Geophilomorpha many short wide segments with telescopic inter- and intra-segmental joints (compare figs 4 and 5 and the two ends of the animal in fig. 3), and neat ways in which the shape of the external armour can be changed, provide a method of obtaining the greatest shape changes per unit length of body, and therefore the most effective burrowing ability. The worm-like *Orya* and *Himantarium* with about 130 segments show a culmination of this tendency. The former can exert a pushing force of 360–400 g./sq. cm. of tergite surface, a figure substantially higher than that exerted by the surface of a burrowing annelid of comparable size, and Pl. 1, fig. 3 shows how *Himantarium* can flatten itself to a ribbon without pushing as it " flows " through tight places, in this instance a slit in a card. A maximum bulk of muscle in these centipedes is diverted to the dorsal, lateral and ventral longitudinal series whose contraction supplies the surprisingly large force.

Many diplopods by contrast exert their thrust upon the soil through the head end, where a skeletal shield, of various sorts (collum, or the first few tergites) transmits the force. The normal use of the legs (Pl. 1, fig. 2) in pushing the body forwards against a resistance is not very different from a pulling action by the legs, and the readiness with which a harnessed diplopod will pull a sledge of weights which it can only just shift is as characteristic of the group as is the possession of diplosegments. Intersegmental joints must be strong, flexible, and longitudinally incompressible if a force is to be effectively transmitted to the front end of an animal. Without the evolution of diplosegments, suitably mobile yet incompressible intersegmental joints could only exist on longer segments, which would mean fewer legs per unit length of body than are present in a typical diplopod. An animal without diplosegments could not exert so strong a push and would be a less efficient burrower (Part 4). Much can be learned by observing animals performing their approximately normal occupations under controlled conditions, and animals cannot be persuaded to carry out quite abnormal performances. The large number of conspicuous morphological characteristics (some 50) which have so far been shown to be associated with certain habits of life (Parts 2–8) indicates that such studies are essential for understanding the divergent evolution of the component groups of the Arthropoda.

Design of Skeleto-muscular Systems.

Skeleto-muscular systems provide mechanisms capable of giving either slow strong movements or quicker weaker ones, since the power of a muscle can be expressed in terms of force, time and displacement. But the two types of movement are mutually incompatible. Strong movements require robust jointing and series of short wide muscles, since the tension generated by a muscle is roughly proportional to its transverse sectional area. It is usually mechanically impossible to combine large displacements with great strength of movement. Rapid movements on the contrary are effected in arthropods by relatively longer muscles giving greater displacements ; the joints between the hard parts are often weak, but allow wide angular movements. The telopodite of the legs of all common fast-running centipedes is not united to the coxa by either a ball and socket, or a tight hinge, or a pivot joint articulation between the hard parts, but by a narrow complex rod of sclerotized cuticle set at right angles to the proximal rim of the trochanter (Text-fig. 1*b*). A more surprising support for a longish leg could hardly be found, yet the elasticity of this minute union contributes to the wide angular displacements of the leg which may reach some 85° ; the strength of this union is sufficient for fast running but entirely unsuitable for strong legs used for burrowing, or for the support of much longer or stouter legs. The weakness of rapidly contracting muscles in fast runners is often compensated for by an increase in their number. The fleet centipede *Scutigera* possesses 33 extrinsic muscles while a strongly pushing iulid possesses but two (Parts 6 and 7).

Slow strong movements are characteristic of Diplopoda, and it is therefore not surprising to find another habit of fundamental importance to this group, that of readily assuming a protective spiral position. The ability to spiral tightly however is the result of extensive modifications at the anterior end of the body, where fewer legs are present on what appears to be the first few diplosegments, so making place for the intucked head. The two habits : burrowing by the motive force of the legs, and spiralling, are both associated with the evolution of the basic trunk characteristics of Diplopoda, which include the nature of the cuticle ; the detailed form of the diplosegments and collum ; the number of segments ; the position of origin, the lengths and shapes of the legs ; the nature of the various types of joints, and the musculature of both body and legs (Parts 4–6).

" The production of the most effective motor system is beyond doubt one of the principal aspects of animal evolution. The mode and rate of locomotion are linked, either directly or indirectly, with all the peculiarities of the body architectonics ". This statement made by Zenkevich (1945), on reviewing the evolution of animal locomotion, could not be more appropriately applied than to the Myriapoda. The most effective motor system in a wide sense involves much more than the various types of gait which are now known to give either fast or strong movements, each type of gait being facilitated by far reaching structural features. Flexibility or rigidity of the body may be equally important. When areas of cuticle are fairly rigid, joints between them are essential, but joints allowing great mobility in all directions, as well as concertina-like contractions and expansions, are usually most undesirable, since musculature must be diverted to restricting flexures in unwanted planes if movements are to be precise, strong or fast. The use of skeleton to restrict movement renders more muscle available for locomotory purposes.

Ball and socket joints are rare in arthropods, and when they occur, as for example between the diplosegments in diplopods and between coxa and body in some insects, much controlling musculature is needed. Comparative myology of chilopods shows the effects of an upper limit to the musculature which one trunk segment can provide ; if great demands are made for a certain type of muscular component, then corresponding economies must be effected in other components. Joints which are expensive in attendant muscles reduce the potential musculature available for effecting direct flexures of the segments of body or limbs, and will not assist an animal to excel in either strength or speed of its limb movements. The bulky geophilomorph muscles which cause the concertina-like shape changes of the body, which can be long and thin or short and thick (Pl. 2, figs. 3–5) allows the existence of little extrinsic limb musculature, and limb movements are neither fast nor strong. The fleet Scutigeromorpha on the other hand have exploited the properties of skeleton and shape of hard parts to the full and drastically reduced the bulk of trunk musculature, so allowing an abundance of extrinsic limb muscles such as is found in no other myriapod.

Very few arthropods have concertina-like bodies such as shown by the geophilomorph centipedes and Onychophora (Pl. 1, figs. 3–5, and Pl. 2, figs. 14–16). The majority have at least an effective " vertebral column " of some sort, dorsal or ventral, skeletal or skeleto-muscular, which fixes a linear dimension along one axis of the body. For example, many Chilopoda and the Symphyla (Pl. 1, figs. 7, 8, and Pl. 2, fig. 12) have in effect a dorsal " vertebral column " which usually does not " let out " when the body flexes in either the vertical or horizontal planes. The greater the number of hinges across a " vertebral column " the easier will dorso-ventral flexure become, and the extra tergites on segments 4, 6 and 8 in the Symphyla (see white arrows on Pl. 2, fig. 11) can together contribute some 75° angular displacement to the very free dorso-ventral flexibility of these animals (Pl. 2, fig. 12). Dorso-ventral bending of this sort is accompanied by a ventral intake of some kind, such as a folding of the segments and this folding is particularly easy in the Symphyla owing to the disposition of the stiffer parts of the cuticle. Provisions such as these are important items in an animal's make up, but they can only be appreciated through a study of living creatures, together with their accomplishments, and with deductions concerning the animal's requirements. That Symphyla are exceptionally able at twisting and turning can be ascertained from observations and comparisons between the photographic records of the activities of many types of animals. Symphyla inhabit leaf mould and mounds of rotten wood, etc., to considerable depths, but their delicate bodies are not suited to burrowing by either the geophilomorph or diplopod method. By very free flexures in all directions Symphyla traverse awkwardly shaped crevices without pushing, and in this habit we have an explanation of the extra tergites diagnostic of modern Symphyla, and can appreciate why this curious feature has been evolved.

It is now generally agreed that the Symphyla stand closer to the insects than do any other living myriapods (Tiegs, 1945 ; Tiegs & Manton, 1958) ; the head structure, segment number and ontogenetic development point to this ; the progoneate condition in Symphyla is secondary (Tiegs, 1945) and the full range of insectan gaits is shown by Symphyla but by no other myriapods (Part 8). The outstanding differences lie in the absence of eyes, the presence of extra tergites and the full series of legs. More speedy running can result from a reduction in leg number and an increase in leg length, and the use of only 6 legs has been evolved independently many times (see p. 64 and Part 2). In respect of segment number the Symphyla could be considered as descendents from the ancestors of insects, and now we can appreciate that the lack of eyes and the presence of extra scutes are specializations correlated with present-day habits of life. Thus no further difficulties lie in the way of accepting the suggestion that the Symphyla and insects have had a common ancestor. Symphyla have remained generalized for a variety of reasons (Part 8), but they have indulged in a few specializations of their own in correlation with their present-day habits. Primitive animals to-day have survived either because they have evaded competition or because they are very competent at something, and in this the Symphyla are no exception.

Limbs as well as the trunk have a need for a fixity of length in certain directions. Distal leg segments in many land arthropods are united by tight dorsal hinges, so that a line passing through them and along the leg always remains the same length, although ventrally the flexed leg is shorter than when it is extended. The proximal limb segments in all animals so far examined are incompressible along a line passing down the middle of the anterior face. These contrivances result in the most advantageous and economical use of the available musculature, whose intrinsic bulk cannot exceed the internal volume of the leg segments. The proximal line or lines of incompressibility enable antagonistic pairs of intrinsic muscles to raise and depress the leg segments. Distal extensor muscles are not required by myriapods or by many other arthropods[2], a remarkable achievement for a leg which exerts a propulsive thrust against the ground during the latter part of the backstroke when the limb is extending ; all available muscles to the distal leg segments are flexor in function, so giving a maximum pull during the first half of the backstroke when flexures are increasing. If distal extensors were needed, as in vertebrates, in crab and crayfish walking legs and in certain myriapod and arachnid joints with specialized movements, the flexors would

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[2] Extension of joints which lack extensor muscles is effected by extrinsic remoter and proximal intrinsic depressor muscles, together with a rotation forwards of the dorsal surface of the leg during the backstroke. (Part 6).

have to be smaller and therefore weaker than they are. The shape and number of leg segments is correlated in great detail with the functional requirements of the animal (Part 6) and it is necessary to appreciate the significance of such structural features before deductions can be made concerning homologies and evolution of leg segmentation in various groups of animals.

Gaits and Body Undulations.

The gaits employed by terrestrial arthropods are becoming well known. Where strong slow movements are needed, as by diplopods when burrowing, the backstroke of the leg is of much longer duration than the forward stroke, and consequently many legs are pushing against the ground at any one moment (Pl. 1, fig. 2, black spots). Where rapid movements are needed, as by fleet centipedes escaping from enemies or pursuing prey, the backstroke may be only 1/10th of the duration of the forward stroke, then very few legs touch the ground at any one moment (Pl. 1, fig. 6, black spots) and stepping also may be fast.

Annelids or arthropods which use many similar parapodia or limbs for either crawling or running exhibit a metachronal rhythm of limb movements. It would be impossible to use all limbs in similar phase, except in special cases, and the result would then be jumping and not crawling ; and if there was no co-ordination between successive limbs the trunk segments would have to be long and the limbs or parapodia short if mechanical interference was to be avoided. The metachronal waves of limb movement which appear to travel either forwards or backwards along the body respectively, determine whether successive legs in the propulsive phase diverge (Pl. 1, figs 2, 7, and Pl. 2, figs. 9, 12) or converge (Pl. 1, figs 3, 4, 6, 8). The exact phase difference between successive legs in annelids and arthropods is of great importance to the animal and is dictated by mechanical needs ; the phase difference is readily changeable with the gait, and the apparent direction of the wave can be reversed by the same animal. It is advantageous for animals to run without any crossing of successive legs, and when this cannot be avoided, owing to the presence of many, not very short, legs, the crossing must take place on the forward swing (as on the right side of Pl. 2, fig. 9). A *Scolopendra* using a "fast" pattern of gait is supported at one or two points on each side of the body only, with 10 successive legs off the ground in the forward stroke (Pl. 1, fig. 6, right side). Such long unsupported stretches of body present mechanical problems to the animal which would have prevented the acquisition of fleetness had they remained unsolved. Legs of a pair must move in opposite phase so that the few points of support for the body are staggered on the two sides ; sagging of the unsupported segments must be prevented so that they do not drag on the ground, but the body must be carried close to the substratum if maximum strides are to be achieved ; and, in contrast to polychaetes, lateral undulations in the horizontal plane must be minimized because their occurrence reduces stride length, and therefore speed, and wastes energy in lateral displacements. The meeting of these needs has involved the whole architecture of pleuron, tergites and trunk musculature of centipedes.

Zoological writings have not infequently referred to powerful serpentine movements of centipedes, assuming that lateral undulations of the body (Pl. 1, fig. 6) provide a locomotory thrust as in snakes. A palaeontologist's speculations even go so far as to suggest the derivation of arthropods as a whole direct from polychaetes via "protoarthropods" exhibiting such movements. The lateral undulations, so conspicuous in the field when lithobiomorph or scolopendromorph centipedes are disturbed, are not shown when the animals move about in a leisurely way ; they are only apparent, and in progressive measure, as the animals attempt to run faster. If these undulations were contributory towards locomotion, a thrust against the ground by the body might be expected, yet a *Scolopendra* can run its fastest over smoked paper with maximal undulations without making a mark on the paper by the body. If *Scolopendra* is suddenly confined laterally when running, it does not exert any lateral pressure by the body against the obstacle, although it may flatten many legs against the flanks to ease its passage. The body may rotate through 90° in order to exert the geophilomorph-like dorso-ventral pushing against the obstacle by becoming thick, but this does not provide speed. As shown in Part 3, undulations only become apparent when the controlling mechanisms break down.

An analysis of the way in which lateral undulations are controlled (Part 7) shows us not only why alternate sized tergites all along the body have been evolved in the three fast running orders of centipedes, but in addition, why the two successive tergites 7 and 8 are both long in all these animals, although the body lengths differ (Pl. 1, figs 6, 7, 8 and Pl. 2, fig. 9). The progressive manifestation of tergite heteronomy in those centipedes most interested in running fast, and doing so with increasing length of leg, is associated with features of the muscles and joints. Horizontal flexures of the joints lying at the anterior ends of the long tergites can be hindered so that only every other inter-tergite joint flexes conspicuously and the region of greatest rigidity lies at tergites 7 and 8 (Part 7). In *Lithobius* each long tergite bears important extrinsic limb muscles from three successive pairs of limbs, and this scute is indirectly united with five sternites, while a slow-moving geophilomorph centipede, in which there is a lesser tendency for the body to undulate, shows only one set of extrinsic limb muscles passing up to each tergite, which is linked with but two sternites.

It appears to be desirable for running myriapods to sense what is before them by turning the head and antennae from side to side ; Onychophora, Diplopoda, Chilopoda and Symphyla do this, often tapping the ground with the antennae. The extra rigidity at tergites 7 and 8, where two large scutes carry many more than their fair share of segmental muscles, effectively damps out the undulations started by the head movements except when the faster gaits are employed, an effect clearly demonstrable by analysis of cinematograph records. *Scutigera* (Pl. 2, fig. 9), the fleetest centipede and with the longest legs, achieves the greatest control of body undulations by fusing tergites 7 and 8, and eliminating half of the other inter-tergite joints by the drastic reduction in size of the short tergites which are invisible in dorsal view, so that in effect two consecutive joints are replaced by one. If undulations were not very well under control, only gaits slower than those actually employed by *Scutigera* could be used without stumbling. The tendency to undulate is mitigated to some extent by a shortening of the trunk segments in *Scutigera* compared with those of *Lithobius* or *Scolopendra*, but this shortening means that limbs must be moved with great precision to avoid mechanical interference with one another, since their fields of movement overlap so extensively (Part 2). This control of flexure at the inter-tergite joints is facultative, more acute flexures at all joints can be seen when animals are cleaning themselves (Pl. 2, fig. 10) or, in the cases of *Lithobius* or *Scolopendra*, curling themselves horizontally into small spaces under bark or stones (Part 7).

Segment and Leg Numbers.

Function will take us far towards an understanding of the variations in segment number in arthropods. The historic arguments as to whether long bodies or short bodies are primitive can be replaced by clear evidence, but the answer is not a simple yes or no, similarly applicable to all groups of animals. An increase in the number of short wide segments in geophilomorph centipedes and in iulid millipedes to some 130 will increase their efficiency as burrowers, but for quite different reasons (Pl. 1, figs 2–5 and see above). A trunk segment number of the order of 20 is small enough for a progressive increase in leg length along the body to help the animal to take maximum strides and not " tread on its own toes " when it runs fast (scolopendromorph centipedes, Pl. 1, fig. 6). Legs, like machines, work most easily when their loading is even and not greatly changing from moment to moment. The loading is almost or quite even during the faster gaits of *Lithobius* and *Scutigera* when only 13 or 14 pairs of legs are used (Pl. 1, fig. 7 and Pl. 2 fig. 9) ; a slightly greater number would produce uneven loading, and the 15th pair of legs in these animals serve either as hooks or posterior " antennae ". The smaller numbers of legs present in the early larval instars of these animals can achieve even loading only when slower patterns of gait are used (Part 3). Thus the addition of segments in later instars permits fast gaits to be employed, an advantage in a pursuit of speed. The evolution of an optimum number of segments is doubtless associated with leg length, muscle physiology and the need for speed by these animals. The several numbers of body segments, precisely fixed or otherwise, in the various orders of millipedes also appear to be correlated with habits (Part 4).

Presumably land arthropods first possessed short legs, perhaps no longer than those of *Peripatus* and *Ayshaeia*. An increase in leg length brought many advantages, not least being the ability to take a longer stride and therefore to run faster. But the possession of many long legs does not permit the use of much variety of gait if stumbling is to be avoided easily, and speed changes have to be done largely or entirely by varying the pace duration (*Ligia* and *Scutigera*) and not by using faster or slower patterns of gait as well (Part 2). A reduction in the number of legs used for walking or running to four or three pairs has occurred independently many times in Crustacea, Arachnida and probably more than once in the various hexapods (Collembola, Protura, Diplura, Thysanura and pterygote insects). This reduction brings many advantages ; legs can be longer still and fanned out so that their fields of movement scarcely overlap, if at all, and a wide variety of gaits is then practicable. Functional requirements also demand that few legs must arise close together and anteriorly (Part 2), and so we can appreciate the significance of the robust thoracic segments, sometimes moving little on one another, of hexapods and the united prosoma of arachnids. Yet a palaeontologist does not hesitate to inform us that the loss of ambulatory appendages " throughout the whole postcephalic body, while it was well adapted to aquatic life, constituted a terrible and unique handicap to those chelicerates that crawled out into the air " without advancing any data in support of the statement. In the absence of precise knowledge of the meaning of animal shapes it has been safe to put forward many unsound comments on arthropod evolution.

Peripatus : An Arthropod.

The anatomy and general habits of the Onychophora have been reasonably well known for a long time, and it is clear that these soft-bodied creatures, possessing a haemocoel and many short legs, exhibit a simplicity of structure which is primitively so and not a secondary degeneration (Part 3). There is strong evidence for the belief that the Onychophora have evolved from the common ancestors of the great myriapod-insect stem (Tiegs, 1945, 1947 ; Manton, 1949 ; Tiegs & Manton, 1958). Yet there are zoologists who affirm that the Onychophora are not arthropods—usually on the grounds of the soft body wall, unstriated muscles and the form of the jaws. No textbook or monograph drops even a hint as to why the Onychophora have retained a soft body wall, while it has been expedient for other classes of arthropods to acquire scutes. The answer to this important question is not far to seek, and it is associated with the occurrence of unstriped muscles and with the form of the jaws.

Deformability of body is more characteristic of some annelids and molluscs than of arthropods. A small garden slug confined behind the head between two plates has no difficulty in moving its body through a gap not much deeper than the thickness of a sheet of bristol board. The lug worm *Arenicola* and *Peripatus* both readily escape though very narrow cracks in a wooden box. Photographs of a specimen of *Peripatopsis moseleyi* extended and contracted are shown in Pl. 2, figs 15 and 16, and the holes (through a sheet of cardboard) next to *Peripatus novaezealandiae* in fig. 14 are all passable to this animal. Selection of a hole to squeeze through is made by explorations with the antennae. The smallest hole shown is about 1/9th of the T.S. area of *Peripatus* when resting, and 20 minutes were taken by the animal to deform the body locally to an even smaller diameter in order to work one leg at a time through the hole all along the trunk. No pushing is exercised, the velvety body bears a delicate sensory hair from the apex of every skin papilla. This feat in deformation could not be achieved by an animal possessing external scutes of any kind (compare fig. 14 with fig. 3 showing the greatest deformability of a scute-bearing arthropod) ; nor with one equipped with a pair of mandibles united by the usual mandibular adductor muscles and tendon (tentorium) ; and this deformability must be recognized as having survival value. In fact it represents a very highly specialized achievement of evolutionary significance which has hitherto not been appreciated. Onychophora can be found in tree-less as well as wooded country, but some of the greatest densities of populations occur deep in decaying logs. If laboratory specimens are confined in small chambers containing food and damp decaying wood fragments, and intercommunicating by narrow passages or cracks, most animals move through one or more of the narrow passages before settling down. This habit under natural conditions cannot fail to lead the animals to rest in places where no predatory chilopod, scorpion or beetle could follow which was large enough to harm Peripatus.

The ability to distort the body resides in the connective tissue " skeleton " situated below the ectoderm on to which the musculature is inserted. This layer shows functional resemblances to coelenterate mesogloea (Chapman, 1953 ; Batham & Pantin, 1951), its configuration being readily altered, although the component fibres probably remain the same length. The fibres are complex in arrangement, their combined thickness being greatest dorsally and least on the legs, and relatively thicker in the larger animals, as might be expected of a skeletal structure. This deformable skeleton ranks as one of the most important specializations possessed by Onychophora. Polychaetes possess a similar but thinner sub-epidermal layer of connective tissue. The cuticle of *Peripatus* appears comparable to those of other arthropods, but is very thin, the outer sclerotized layer being too thin to provide rigidity. Sclerotized cuticle is important because it carries hydrofuge lipoids (Blower, 1951), but it does not stretch. A caste cuticle of Peripatus floated on to water has a 17% greater area than the apparent surface area of the animal from which it came. The part of the cuticle which is absorbed by minute furrows between sensory papillae, giving the velvety appearance of the animal, allows great shape changes of the body to be associated with a very hydrofuge, sclerotized, but unstretchable outer cuticular layer. That Onychophora do not lack the ability to form thick sclerotized cuticle, which is consequently stiff, is shown by the presence of claws, jaw blades and long hollow apodemes for the insertion of jaw muscles (Manton, 1937). However, an elaboration of either subcutaneous collagen or the evolution of cuticular scutes was probably an early parting of the ways between Onychophora and other Arthropoda.

Slowness of movement is desirable in animals whose bodies suffer great deformations, such as sea anemones (Batham & Pantin, 1950) and the slowness of onychophoran movements similarly avoids sudden or large changes in haemocoelic pressure when deformations are great. But the absence of striated muscle in limbs and trunk of *Peripatus* also is associated with an ability to deform the body extremely. Unstriated muscle fibrils may contract by 400–500 per cent. (Batham & Pantin, 1951) but striated muscle frequently contracts by but 20 per cent. or less. It is unlikely that an animal equipped with striated muscle could achieve the range of deformations shown by *Peripatus* ; secondarily soft bodied arthropods do not do so. The retention of the unstriated muscles of an annelid-like forbear must have been essential for the exploitation of the habit of squeezing through awkward places which appears to have been of great survival value.

The jaw movements of *Peripatus*, so like the stepping movements of the legs (Manton, 1937), may be primitive, and have probably been preserved because the evolution of mandibles, which bite in the transverse plane and are supported internally by tendon and endo-skeleton, was incompatible with squeezing through cracks. Even the head of *Peripatus* can pass very narrow places where a slug may be halted by the size of its odontophore.

Thus the three onychophoran characters which have been held as evidence against the arthropodan nature of these creatures are directly associated with habits of life of fundamental importance, and do not withhold the arthropodan status from the group. Further, the gaits of *Peripatus* are more generalized than those of any other class of arthropod. The more specialized gaits of the various myriapod and hexapod groups could readily be derived from gaits such as those of *Peripatus* (Parts 1–4). The persistence of primitive undeveloped gaits in an animal whose star turn is neither running nor pushing but squeezing without pushing, is readily understandable ; it is also possible that a connective tissue skeleton is not sufficiently firm to permit either the strong slow movements or the quicker ones associated with the more specialized gaits of other arthropods. A consideration of habit greatly advances our understanding of the structure of these " living fossils ".

Scutigera : A Specialized, Not a Primitive Centipede.

Onychophora and Symphyla are not the only arthropods which derive protection from awkward crevices ; indeed, it is only the longest-legged or the winged arthropods which avoid this type of hiding place. Millipedes eat and push their undeformable bodies through an abundance of decaying vegetable matter, but most centipedes seek their elusive prey partly in the open and partly in crevices. Chilopods when caught are nearly always hungry, while diplopods are seldom in need of a meal. Getting into crevices which are wide enough to take the laterally projecting legs of chilopods is assisted by the soft pleuron allowing some dorso-ventral flattening. The tergites and sternites of the *Lithobius* shown in Pl. 1, fig. 7 can be pulled together sufficiently for the animal to pass the gaps shown. The width of the head and poison claws is about twice that of the larger gap, and were it not for considerable specialization of head, mouthparts and poison claws the head could not pass through so small a space. Not only can the head pass, but the poison claws and second maxillae, which grip the prey can move in the horizontal plane and manipulate food in so shallow a crevice. The head itself is very flat, the antennae arise anteriorly, not dorsally, and the joints of the poison claw are very neatly contrived (Pl. 2, fig. 13).

Scutigera on the contrary feeds in more open spaces and predominantly on flies etc. and the head has clearly never been specialized by flattening as in other centipedes. A *Scutigera* equal in weight to *Lithobius* cannot traverse so shallow a slit (Pl. 1, fig. 7). Fahlander (1938) has drawn attention to some primitive features of the head of *Scutigera*, the dome shape with dorsally arising antennae much as in primitive insects, the more elongated and leg-like form of the poison claw and second maxilla, and the more primitive state of the former with a separate sternite (Pl. 2, figs 9 and 10). The movements executed by these mouthparts are more ventrally directed and can be considerably varied, and the joints of the poison claw are not so specialized for working in a dorso-ventrally confined space. The primitive state of the head has led Fahlander (1938) to believe that the Scutigeromorpha are the most primitive centipedes. A functional analysis of the trunk morphology (Part 7) on the other hand indicates that the group is the last word in centipede advancement and specialization, and we are not surprised to find compound eyes only in these most fleet and agile of all centipedes.

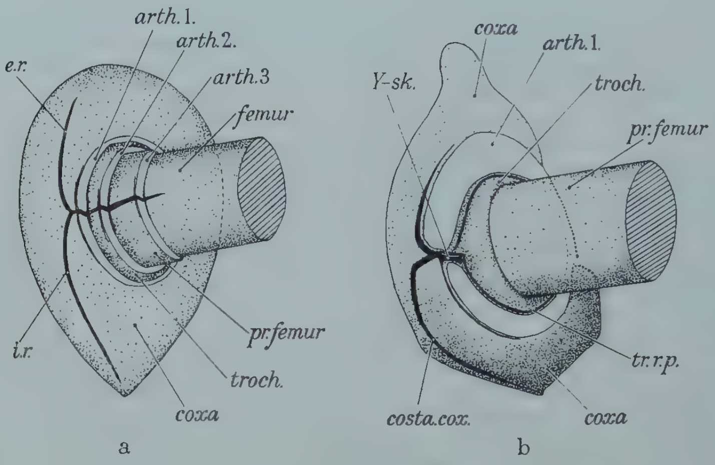
This seeming contradiction in conclusions drawn from the head and from the trunk is explicable on the feeding habits. *Scutigera* appears never to have been adapted for hunting and feeding in very shallow crevices, as have other centipedes ; its longer legs, conferring its great speed of running, do not lend themselves to moving rapidly in crevices, in contrast to scolopendromorph and lithobiomorph centipedes. *Scutigera* can lower its body most expertly into small depressions and slowly fit itself, legs and all, into quite small cracks during the many hours when it is hiding and not hunting, but it cannot run rapidly in such places as can the shorter-legged centipedes. We can but suppose that the ancestors of *Scutigera* were always more open in their habits, even before they acquired their superlative specializations associated with long legs (Part 7), and that they thereby avoided the head specializations seen in other groups of centipedes.

Habit Reversals and Their Consequences.

The search for the functions of morphological characteristics of animals is often greatly helped by comparisons between different groups. Some arthropods, like humans, appear to have become " dissatisfied " with what they have achieved and have embarked upon opposite habits. Such reversals are correlated with structural modifications superimposed upon an earlier morphology associated with the opposite type of habit. The most significant habit concerned with the evolution of Diplopoda is that of obtaining cover and food by pushing into the substratum. Subsequent changes in the exact method of pushing and in the perfection of secondary accomplishments appear to be associated with the morphology of the various orders. The Lysiopetaloidea however have abandoned their basic pushing habit in favour of fleetness and carnivorous feeding. The angle of swing of the leg has been increased at the expense of the strength of the coxa-body articulation ; the appearance of long extrinsic limb muscles gives increased displacement at the leg joints, while the normal short extrinsic muscles usually supplying strength are reduced ; long intrinsic muscles traversing many segments replace the typical diplopod series of short muscles, and many convergencies towards the morphology of the fast-running centipedes are seen in the muscle topography. The study of animals such as the Lysiopetaloidea provides additional evidence as to the significance of muscle and joint morphology in typical pushing diplopods and in fast-running chilopods, besides giving clear indications as to the phylogeny and changing habits of the Lysiopetaloidea themselves (Part 6).

Among the centipedes there is one outstanding example of habit reversal coupled with changed morphology, but the full significance of the reversal has not yet been elucidated. Through the kindness of Professor V. V. Hickman I have been privileged to keep *Craterostigmus tasmanianus* in captivity, a centipede allied to *Lithobius* and found only on some mountains in Tasmania and the South Island of New Zealand. Pocock (1902) described the animal as possibly intermediate between lithobiomorph and scolopendromorph centipedes and regarded the former as creatures in which every other segment had been more or less eliminated, complete with legs ! He did not consider, from the functional aspect, how or why such an astonishing change could have come about. Attems (1926) and others have rejected this idea and have appreciated the correctness of placing *Craterostigmus* within the Lithobiomorpha. The basic morphology is clearly that of *Lithobius* with a pronounced degree of tergite heteronomy and a similar number of body segments and limbs, but the segments are much longer and thinner, so that the overall proportions are more like a scolopendromorph than a lithobiomorph centipede (Pl. 1, figs 6–8). The most curious features of *Craterostigmus* are all associated, directly or indirectly, with a secondary increase in the ease of horizontal flexing of the body. Each long tergite is divided into large anterior and small posterior scutes, and the latter overlap the scutes lying in front and behind them, a device facilitating flexure at the joints, and also found just behind the head in some scolopendromorph centipedes. Pleural scutes have been rearranged to give bending along a vertical line level with the extra dorsal joints. This has weakened the normal support for the coxa, an effect compensated for in a unique manner, but leaves the coxa far less mobile than in other centipedes (see Part 7). *Craterostigmus* can only run slowly, and by slow patterns of gait which bring the points of support of the body much closer together than in the fast gaits of *Scolopendra* (compare the distances between the black dots on Pl. 1, figs 6, 8). Very intense illumination can momentarily stimulate *Craterostigmus* to try to run faster by using a slightly faster pattern of gait in which the points of support of the body are further apart, but crossing of successive legs in the propulsive backstroke and uncontrollable undulations of the body bring the effort to an end.

What this increased flexibility in *Craterostigmus* is used for in natural circumstances is as yet not fully known. One suspects that the advantage must be great for the whole trunk morphology to have been changed in this way and the ability to run fast to have been abandoned. The animal lives much as do many Scolopendromorpha, but in wetter places, within decaying logs etc. The long flexible body allows *Craterostigmus* to curl round its eggs and guard them as the Scolopendromorpha do ; *Lithobius* cannot do this, its shape and jointing being unsuitable, and the eggs are



TEXT-FIG. 1.

Diagrams to show a striking convergent resemblance between a leg joint of (*a*) a diplopod *Polyxenus* and (*b*) a chilopod *Lithobius* which is the result of a pursuit of speed and not strength of movement.

The coxa, frequently cylindrical and articulated with rigid trunk cuticle, is so widened proximally in these animals that much or all of the coxa forms a broad plate almost flush with the body surface, and the proximal rim fades into arthrodial membrane on the trunk (Parts 5 and 6). The only firm union between the more distal leg segments and the coxa is a narrow Y-shaped sclerotization (black) which crosses the arthrodial membrane *arth*. 1. between coxa and trochanter on the anterior face of the leg, and spreads its two arms across the coxa, the lower as the " costa coxalis " of hitherto unknown significance in the Chilopoda, and as the internal and external rami *i.r.*, *e.r.* of the previously recognized " ornament " on the leg of *Polyxenus*. In both, the trochanter is of much smaller diameter than the distal part of the coxa, and the ample arthrodial membrane *arth*. 1. between them permits very wide excursions of the trochanter except at the elastic sclerotized bar. In *Polyxenus* similar joints separate the next two leg segments (the prefemur *pr.fe.* and femur *fe.*) and the stem of the Y-shaped skeleton fades out on the femur and sends short branches round the proximal and distal margins of the segments as shown. In the fast running Chilopoda the trochanter and prefemur are fused, the stem of the Y-shaped skeleton is short and set at right angles to the proximal rim of the trochanter, where it is associated with a substantial annular sclerotization passing round the proximal rim of the trochanter, an exaggeration of the weaker branches of the Y-skeleton of *Polyxenus* in similar situations. The three flexible arthrodial membranes between segments of markedly different diameters *arth*.1, *arth*.2., *arth*.3 of *Polyxenus* provide a combined flexibility comparable to that of the chilopodan single large arthrodial membrane, *arth*.1. This remarkable jointing in both cases allows large angles of swing of the leg, permitting long strides, but this is achieved at the expense of strength of articulation, and therefore is suitable for weak fast movements only. The details of body structure of *Polyxenus* indicate that this diplopod has changed its habits and abandoned its basic ability to exert strong leg movements, and in principle has reached a similar solution to that evolved by the Chilopoda in meeting a similar need.

rolled in soil, one at a time, by the gonopods. *Craterostigmus* lacks gonopods, presumably by loss owing to changed habits, but the life cycle remains anamorphic as in *Lithobius*. The food of *Craterostigmus* is unknown, and alone among centipedes of my keeping it has not survived more than a few weeks in captivity, because it refused all the animal food offered to it on which all other centipedes have thrived.

The problems raised by the habits of *Craterostigmus* reach a more difficult level than those already considered. We must search for the significance of a performance which is not a simple matter of being possible to one animal and impossible to another, such as pushing for a millipede and fast running for a centipede. *Craterostigmus* has evolved a very elaborate way of flexing its body more *easily* than its lithobiomorph ancestors could do, but *Lithobius* can flex remarkably acutely when curling into a small place of hiding, although not so acutely as can *Scolopendra*, but flexures in *Lithobius* are well under control during moderately fast running. The advantage of mimicking the flexibility of a *Scolopendra* must have been great if in doing this the power to control body undulations was lost.

Conclusions.

The functional significance of a sample of the outstanding structural features peculiar to various groups of arthropods has been touched on above, but fuller treatment, presented elsewhere in this journal and in course of preparation, is necessary to establish the conclusions reached. Information of this kind not only enables us to appreciate the significance of hitherto rather meaningless animal characteristics, but enables us to distinguish between primitive and specialized morphology, real affinity and otherwise. Structures associated with outstanding specialized performances can hardly be primitive. Comparative anatomy and performance together indicate precisely the nature of the advances, both structural and functional, which have been achieved by various groups of animals. We gain clear evidence not only of these achievements, but what is equally important, an appreciation of the stages which must have been passed through in the course of their evolution. We can distinguish between the parallel evolution of functionally comparable features, and a similarity due to close affinity. Convergent similarities of structure and habit may be reflected in the whole animal, such as the resemblance between *Scolopendra* and *Craterostigmus* (Pl. 1, figs 6, 8), or they may be seen in a certain organ only, the animals' general form being very different. The remarkable resemblance between the coxa-trochanter joint and the form of the coxa in the millipede *Polyxenus* and in all centipedes is a striking example (Text-fig. 1 and Parts 5, 6, 7). *Polyxenus* is not intermediate between diplopods and chilopods as has at times been suggested, it is basically diplopodan in structure, but its legs have superimposed convergent resemblances to those of chilopods in respect of the need for a large angle of swing of the leg. These detailed studies on the Myriapoda, covering all the conspicuous diagnostic characteristics of the trunk and legs, are an essential preliminary towards an understanding of the evolution of the great groups of hexapodous arthropods which, above all other invertebrates, dominate the land.

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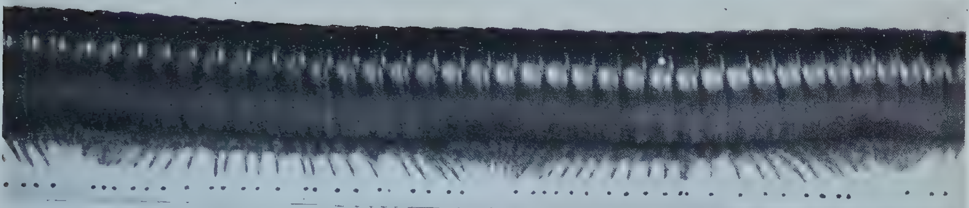
DESCRIPTION OF PLATES.

The descriptions of the photographs are intended to indicate the major correlations which exist between structure and function in the various groups of myriapods which are illustrated; all structural features mentioned are associated with habits of evolutionary significance. The phase difference between successive legs, " p.d." is expressed as that proportion of a pace by which leg $n + 1$ is in advance of leg n. When this is $< 0·5$ consecutive propulsive legs diverge and the metachronal wave appears to travel forwards over the body. When the p.d. is $> 0·5$ consecutive propulsive legs converge and the waves appear to travel backwards over the body. The figures in brackets give the relative durations of the forward and backward strokes of the legs. Black or white dots level with legs indicate that their tips are on the ground during the backstroke, and black or white arrows show the positions of joints between two tergites belonging to the same segment.

PLATE 1.

FIG. 2.—A iuliform millipede (Diplopoda) (295 mm.) performing a slow gait giving a strong push at the head end where a suitably shaped scute, the collum, transmits the thrust ; the cuticle, except at the joints, is rigid. About half of the body length is seen in side view. The body segments are fused in pairs (diplosegments), the cuticle forming complete rings, each bearing two pairs of legs. The inter-diplosegmental joints are mobile but non-telescopic, and thus transmit the forward thrust ; strong muscles between the diplosegments maintain any momentarily suitable body curvature. The evolution of short deep diplosegments and many of them gives the large number of legs per unit length of body which supplies a maximum pushing force. The two metachronal waves of limb movement in the photograph show 20–22 consecutive legs performing the propulsive backstroke and 8–10 legs off the ground during their forward stroke. This disposition results from leg movements in which the backstroke is of much longer duration than the forward stroke, and the phase difference between successive legs is small : gait (3·0 : 7·0), p.d. 0·03 approx. If this phase difference was larger, the waves would be shorter, and only less strong patterns of leg movement could be used (Part 4), and if the p.d. was $> 0·5$ (metachronal waves travelling backwards) the successive propulsive legs would converge and cross each other instead of fanning out, a mechanical impractibility to this animal.

FIGS 3, 4 and 5.—*Himantarium* sp. a geophilomorph centipede (Chilopoda), expert at burrowing, 222 mm. long when extended. A soil crevice is widened by a local thickening and shortening of the body, the thrust being supplied by body muscles and not by limbs. The whole animal is shown in fig. 3. The anterior half of its body is actively walking forwards, the segments here being elongated, and the posterior half of the body is longitudinally contracted and lies in a loop, and the legs are here stationary and roughly parallel with one another. The dorso-ventral thickness of the body is seen near the posterior end. The slit



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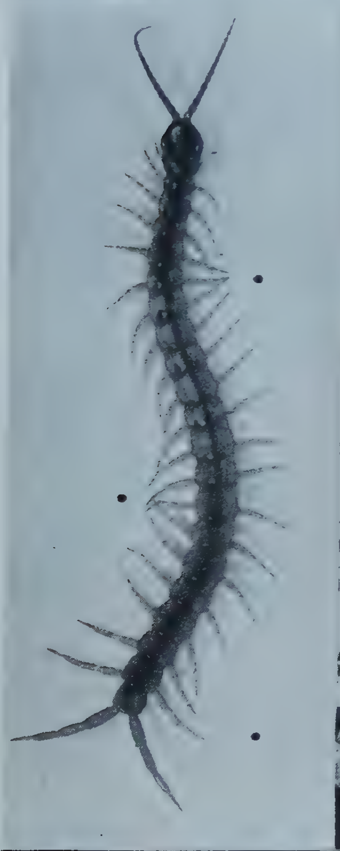

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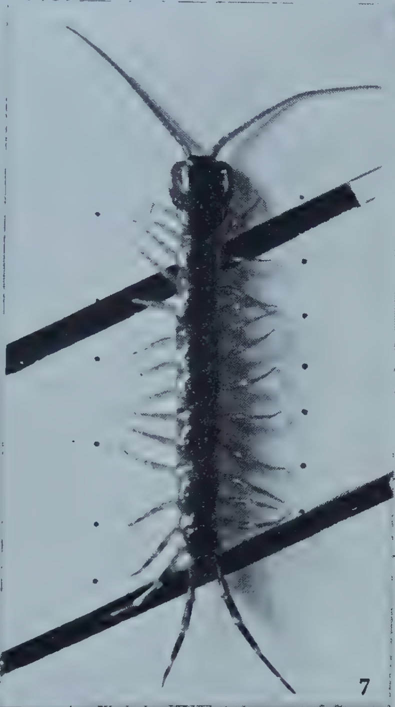

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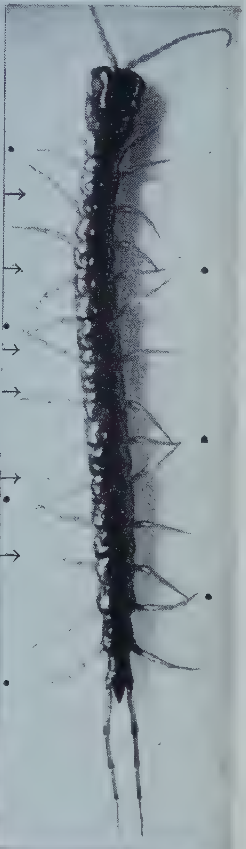

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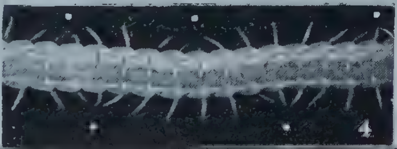

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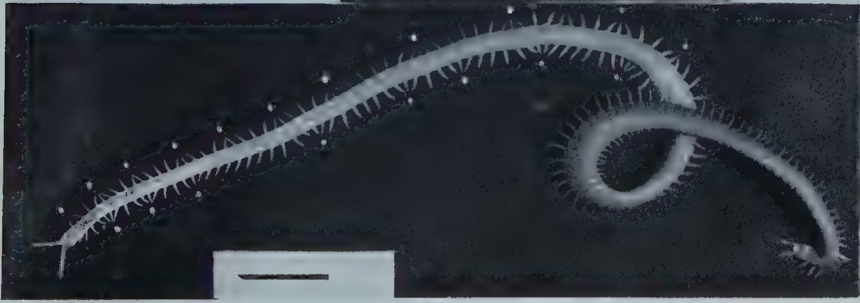

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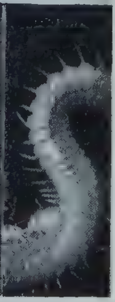

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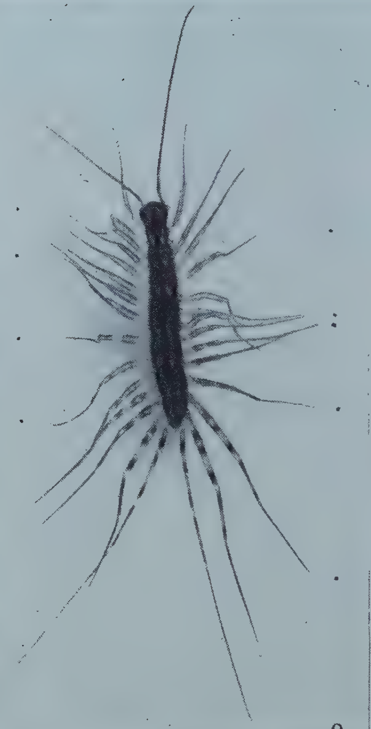
Diplopoda and Chilopoda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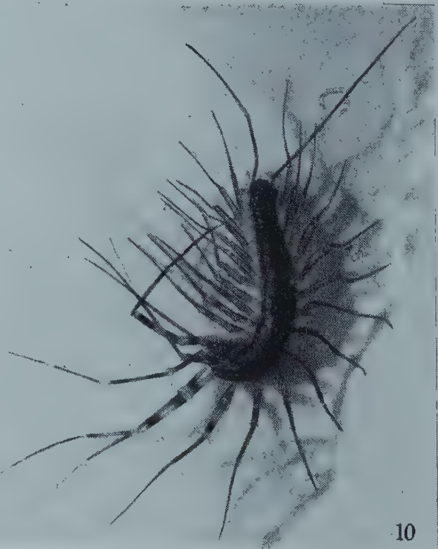
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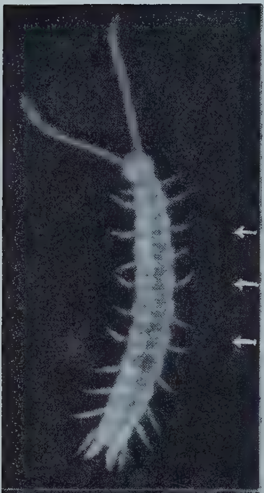
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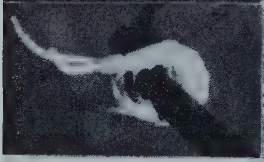
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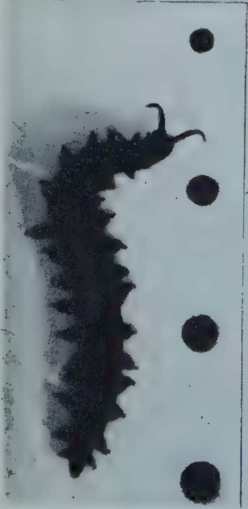
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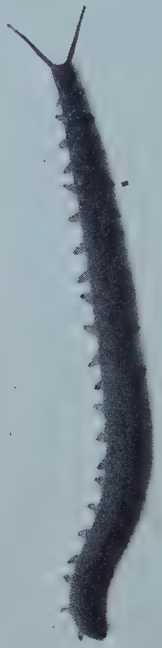
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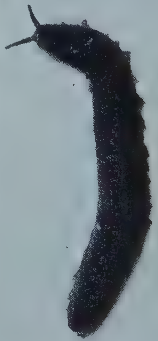
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Symphyla, Chilopoda and Onychophora

in the piece of white card shows the smallest gap through which the animal can pass by dorso-ventral flattening. Figs 4 and 5 show the same body segments (× 1·6), elongated in fig. 4, displaying a principal and an intercalary tergite (dorsal scutes) corresponding with each pair of legs, and in fig. 5 the body is much wider and the segments shorter, each principal tergite completely overlaps each intercalary tergite, and the principal tergite is apparently shorter than in fig. 4 because it is arched more convexly. The large number of fairly short segments, each with two telescopic joints, and many details of skeleton and muscle, give an ability to burrow more deeply than is possible to iuliform millipedes, but limbs are short and fast running is impossible (see Parts 3 and 7).

FIG. 6.—*Scolopendra cingulata*, a fleet centipede (Chilopoda) 110 mm. long, running as fast as it can; speedy movements are used for the catching of prey and escape from enemies. Fleetness is achieved by quick stepping and by leg movements in which the propulsive backstroke is very much faster than the recovery forward stroke, gait (8·5 : 1·5), thus very few legs are in contact with the ground at one moment. Legs of a pair move in opposite phase, and so the points of support of the body on the two sides are staggered. Movements are weak but rapid. Successive legs are put down on almost the same footprints, marked on the photograph by black dots. Only right legs 5–7, 18–20 and left legs 12–14 touch the ground, the body is supported at these three points only and 10 consecutive right legs are off the ground. p.d. approximately 0·92.

The utilization of a p.d. of $> 0{\cdot}5$, giving a backward transmission of the metachronal wave (in contrast to that in fig. 2), results in convergence of usually 2–3 successive legs during the propulsive backstroke, as in figs 3 and 4; the small leg length relative to segment length avoids any conspicuous crossing of the the legs, and the use of this type of phase difference may minimise the tendency towards lateral undulations of the body (see Part 7). Undulations of the body in the horizontal plane are conspicuous (none occur at slow speeds when the gaits used bring the points of support of the body closer together, as they are in the animal shown in fig. 8); these undulations reduce the potential speed, and their manifestation is hindered by the evolution of tergites of alternate length and associated musculature which reduces flexures at the anterior ends of the long scutes. The two successive long tergites 7 and 8 form the most rigid part of the body where in slow running the undulation induced by a sensory casting of the head from side to side is effectively damped out (see Part 7). The presence of only 20 pairs of running legs allows each leg to be appreciably longer than the one in front (cf. figs 2 and 3); this facilitates stepping without stumbles due to interference of one leg by the next (Part 3). Great flexibility of the pleuron is essential for the execution of leg movements giving a large angle of swing, and consequently a long stride (Parts 6 and 7). The greater leg length than in Geophilomorpha (figs 3–5) facilitates speed but limits the burrowing ability, as does the lesser deformability of body shape.

FIG. 7.—*Lithobius forficatus*, a fleet centipede (Chilopoda), 25 mm. long, which catches flies and other fast-moving prey, and shelters under bark and in relatively wider crevices than those negotiable by *Scolopendra*. The photograph shows slow running without body undulations, gait near (5·5 : 4·5), p.d. 0·16. The scale of the figure gives approximately the same segment volume as that of *Scolopendra* in fig. 6. The upper slit is freely passable to the animal while the lower one can be passed only with difficulty, the pleuron is flexible and dorso-ventral flattening occurs, but not to the extent possible to *Himantarium* (figs 3–5). Only 15 leg-bearing segments are present, and 14 pairs of legs are used for the gait shown. Leg length is greater than in *Scolopendra*, leg 7 of *Lithobius* being about 33 per cent. longer than that of *Scolopendra*, and each leg is longer than the one in front, so spreading the footfalls, which helps to avoid stumbling. Tergite heteronomy in length is much more marked than in *Scolopendra*; the two long 7th and 8th tergites, the most stable part of the body, now occupy a central position between head and tail. Body undulations occur at fast speeds, but are more under control than are those of *Scolopendra* as a result of the very marked heteronomy of tergites and of muscles, and the shorter, wider segments; faster gaits than shown in fig. 7 result in crossing of successive legs in the forward recovery stroke (Part 3, Pl. 34, fig. 36). The use of a phase difference between successive legs of $< 0{\cdot}5$ is obligatory to avoid crossing of legs during the propulsive backstroke (Part 3). The use of 14 pairs of legs results in even or almost even loading of the legs during the propulsive backstroke. With fewer legs (young instars), even loading can only be obtained from the use of slower patterns of gait, and uneven loading would also result from the use of more than 14 pairs of legs performing the faster patterns of gait. Thus the exact number of trunk segments in Lithobiomorpha brings functional advantages.

FIG. 8.—*Craterostigmus tasmanianus*, a curious lithobiomorph centipede 46 mm. long, from Tasmania, in which the ability to run fast and control lateral undulations of the body has been sacrificed in the acquisition of a secondary increase in lateral flexibility due to subdivision of the long tergites at the points indicated by the arrows, and by pleural modifications. The scale of the photographs is that giving the same body weight as *Lithobius* (fig. 7). *Craterostigmus* runs on 14 pairs of legs, but the segments are so elongated that a phase difference between successive legs of $> 0{\cdot}5$ of a pace can be used without resulting in crossing of propulsive legs. Gait (5·5 : 4·5), p.d. 0·75.

PLATE 2.

FIGS 9 and 10.—*Scutigera coleoptrata* (22 mm.), the fleetest of all centipedes (Chilopoda), preying on flies, etc., running rapidly over rock surfaces and walls, hiding in small crevices, but unable, owing to length of legs, to penetrate into soil and narrow channels passable to geophilomorph and scolopendromorph centipedes or the spaces wide enough for *Lithobius*. Almost the same gaits as those of *Lithobius* are used, and for the same reasons. In fig. 9 the animal is running very fast (*c.* 500 mm. p. sec.) by gait (6·6 : 3·6) and p.d. 0·14 approx., but very little body undulation is apparent. A great tendency to undulate at fast speeds, owing to the leverage of the long legs, is countered by a further shortening of the segments, compared with *Lithobius*, and by an exaggerated heteronomy in tergite length (and in muscles) so that only 7 tergites lie over the 14 pairs of running legs. Long tergites 7 and 8 are fused, and they and tergites 1, 3, 5, 10, 12 and 14 cover over the minute intervening scutes. The dorsal respiratory chambers appear as light sub-median areas at the posterior end of the long tergites. The progressive increase in leg length along the body is more marked than in *Lithobius* ; this enables the legs to be fanned out anteriorly and posteriorly, so spreading their overlapping fields of movement (Part 2) and facilitates stepping ; right legs 5, 6, 11, 12 and 13 are on the ground and the footfall of leg 11 lies far outside and almost level with that of leg 6, four legs in the recovery phase (legs 7–10) cross over each other in the intervening space (right leg 2 has been detached at its breaking plane across the trochanter). The very long 15th pair of legs function as posterior " antennae " during backward progression. Anteriorly and posteriorly directed setae, which may be proprioceptive, can be seen at the distal ends of the femur and tibia ; stepping must be very precise if stumbling is to be avoided. The sure-footedness of the animal is due to plantigrade stepping on many segments of the much divided tarsus, all of which are provided with gripping hairs, in contrast to the stepping on the tip of the tarsal claw in other centipedes and millipedes (Pl. 1). The head is dome-shaped, bearing dorsally inserted antennae, in contrast to other centipedes (fig. 13) and not at all suited to feeding in narrow places; the edges of the weak poison claws show beside the eyes (cf. *Lithobius* and *Craterostigmus* Pl. 1, figs 7, 8).

FIG. 10.—*S. coleoptrata* resting and cleaning its legs. Left leg 12 is being passed between the mouthparts, the tips of the maxillary palps are turned back (cf. fig. 9) as they manipulate the limb. The curvature of the body, which is not maximal, shows that the control of horizontal undulations during running (fig. 9) is facultative and not due to permanent rigidity of the trunk.

FIGS 11 and 12.—*Scutigerella imaculata* (Symphyla), 4 mm. long. An agile animal penetrating certain soils by a great ease of bending in all directions, but not by pushing. In surface running *Scutigerella* gains protection by intermittent darts and the execution of acute " hair pin bends ", changing direction more sharply and rapidly than is possible to small predatory arachnids etc. The flexibility of the trunk is enhanced by the divided tergites on segments 4, 6 and 8, white arrows showing the position of the extra dorsal joints. All tergite joints give great horizontal mobility and the extra dorsal joints aid dorso-ventral bending. The sternal region folds freely between its isolated scutes. The first trunk leg is short and here invisible, legs 2–12 are ambulatory, much the same in length, and shorter than those of any but the burrowing centipedes ; the gaits are such that differential leg length would bring no mechanical advantage, as to Scolopendromorpha, Lithobiomorpha and Scutigeromorpha. The 13th legs form posterior cerci and the 14th are represented by trichobothria not visible in the photograph. The 14 trunk segments correspond with the basic segment number in insects ; the shortness of symphylan limbs is correlated with their crevice-soil habits ; and the gaits employed represent the slower end of the series shown by the Scolopendromorpha, and correspond in great detail with those shown by insects (Part 8).

FIG. 12.—*S. imaculata* running round a plant fibre.

FIG. 13.—*Scolopendra cingulata* (Chilopoda), side view of the head of a narcotized specimen to show the great flattening of the head capsule, with antennae arising anteriorly and not dorsally, and the large poison claws which bite in the transverse plane close under the head, instead of swinging antero-posteriorly as do the walking legs. The poison claws of *Scutigera* are intermediate in form and in movements between the walking legs and poison claws of *Scolopendra*. The head, mouthparts and poison claws of *Scolopendra* are together less deep than the body, so enabling the manipulation of prey in very shallow crevices.

FIG. 14.—*Peripatus novae-zealandiae* (Onychophora). All the holes in the card are passable to the animal. It walked rapidly through the largest hole and took 20 minutes to deform itself, one leg at a time, in passing through the smallest hole, diameter 2·5 mm.

FIGS 15 and 16.—*Peripatopsis moseleyi* (Onychophora), the same specimen extended (60 mm.) and walking fast in fig. 15 and contracted and resting in fig. 16. Unlike other Myriapoda which use common footprints, leg $n + 1$ is put on the ground after leg n is raised (fig. 15, left leg 15 is raised before leg 16 is put down), and not before this event as in figs 3, 4, 6, and 8, a type of stepping necessitated by the thick blunt shape of the legs, and unsuitable for faster running by the pointed legs of other arthropods (Parts 1 and 2).

CHROMOSOMES AND FERN PHYLOGENY WITH SPECIAL REFERENCE TO "PTERIDACEAE"

By I. MANTON.
(*Professor of Botany, Leeds University.*)

(With Plates 3 and 4 and 4 text-figures)

Introduction.

Since 1950 a large and rapidly growing body of accurate cytological data has become available for the first time for the Pteridophyta, but since chromosome numbers, like any other morphological character, require phyletic interpretation it is perhaps relevant, in the Darwin-Wallace centenary year, to draw attention to some of the evolutionary problems which they raise and to others which they may help to solve.

Pteridophyte taxonomy has had a long history, much of which was surveyed in the centenary publication of the California Academy of Sciences prepared in 1951 and which therefore need not be repeated. The effective application of cytology to solving problems in fern taxonomy is, however, so recent that it could not be adequately discussed at that date. The fact that we can now begin to do so is partly due to the post-war developments in air transport which have made tropical floras (and their cytology) accessible to Europe on an entirely new scale, and partly to a revival of interest in fern classification by herbarium botanists. This revival of interest is expressed by the publication, within a space of seven years, of no less than three independent systems of classifying the more modern ferns (Ching, 1940; Holttum, 1946; Copeland, 1947) after an almost complete gap[1] since 1902, the date of the fern volume of Engler & Prantl. The years between these dates are dominated by the life work of Carl Christensen (*Index Filicum*, 1906 with supplements 1913, 1917, 1934) and of Bower (*Origin of a Land Flora*, 1908, *The Ferns*, 1923, 1926, 1928). Both these great botanists have made an indelible mark on their times and in different ways have been part of the stimulus behind the present renewal of interest. Their approach has, however, been so different that, with the current twentieth century tendency to regard herbarium botany as, somehow, inferior to laboratory botany, it is doubtful whether a valid appraisal of the importance of either can yet be made. It is, however, certain that the botanical world in general is far more conversant with the ideas of Bower than with those of Christensen and it is therefore perhaps important to emphasize the special significance of the contribution of pure taxonomy to understanding of the Pteridophyta at the present time.

Laboratory botany of the nineteenth and early twentieth century has been indispensable for sorting out morphological concepts without which major phyletic sequences can neither be detected nor interpreted. The important contributions of Bower to the phyletic interpretation of the more ancient and more primitive ferns is beyond dispute, but an essential part of this success is due to the relatively small numbers of extant representatives. When the undoubtedly ancient ferns (discussed in Bower's *Ferns*, vol. 2) are removed we are left with 200 genera and over 7000 species out of a world total of some 300 genera and 10,000 species. Moreover, almost all these are tropical, with nine out of every ten genera confined to the tropics and with no temperate representatives of any kind. In dealing with these, the laboratory botanist working in Europe with access to no more than the limited local flora, eked out by a botanic garden, is at an almost hopeless disadvantage. The large world herbaria on the other hand are repositories of material from tropical lands accumulated without theoretical bias, but posing all the detailed practical difficulties with which taxonomy is designed to deal. Our more modern requirement that taxonomy should also express phylogeny cannot in practice be pursued effectively much beyond that point to which the herbarium botanist has reached and therefore the greatest need for further understanding of the mass of modern ferns in the mid-twentieth century has been for a considered restatement of the views of the experienced practical systematist, notwithstanding, or indeed perhaps because of, the existence of Bower's *Ferns*, Vol. 3.

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[1] A precursor of this renewed activity is of course Christensen's chapter on the Filicinae in Verdoorn (1938) in which he summarises an attempt at a new classification based on his own unrivalled knowledge of " four-fifths of all known ferns ". This summary is one of Christensen's last works and it was never fully elaborated. His ideas have, however, greatly influenced those of all subsequent writers.

That we now have three such statements with a prospect of others to follow all differing in quite substantial features only underlines the urgency of the need. The nature of the disagreement should not, however, be misinterpreted. There is no divergence on the fundamental view that the " Polypodiaceae of authors " (i.e. the 200 genera and over 7000 species referred to above) are polyphyletic, although, as recently as 1940, this had to be explicitly stated by Ching as if it were a new conclusion. That within less than a decade finality was not reached in unravelling the exact details, or even the exact number, of all the phyletic lines is scarcely surprising especially when it is remembered that ferns offer no ready-made complex of taxonomic characters comparable to those so conveniently provided by floral morphology in flowering plants. The change-over from the single character classification of Linnæus to a grouping based on a complex of characters (i.e. the arrangement of floral parts on the receptacle), and for this reason able to withstand the impact of Darwinism when it came without being totally disrupted, was achieved in flowering plants quite early in the nineteenth century (cf. de Candolle, *Regni vegetablis*, 1819–22). In ferns the search for a suitable complex to replace the single character is still proceeding, and, in the effort to find it, an increasing number of criteria have been brought into use. It is no accident that while Copeland (1947) starts his key to fern families with spore, sporangial, and soral characters of a fairly conventional kind he ends with details of venation, spore shapes, presence or absence of idioblasts etc. Ching (1940) actually starts his key with stem anatomy, whilst Holttum (1946, 1949, 1954), having a wider knowledge of living tropical plants, both wild and cultivated, than any other recent systematist who has been deeply concerned with these problems, has stressed a number of unusual details in the structure of hairs and in leaf architecture which accounts to a considerable extent for the divergence in treatment. As long as family boundaries are uncertain there is no other way of clarifying the position than by investigating every structural feature no matter how small, which lends itself to precise description, and then to search for groups of characters which occur together. At any moment a chosen group of characters may show itself to be insufficient for the detection of parallel evolution, and additional criteria may be needed to do so. Such criteria are increasingly drawn from the less conspicuous and the less obviously adaptive characters, to perceive which, amongst the ferns, requires not merely taxonomic training but extensive tropical experience. The special timeliness of each and all of the revised systems mentioned, to serve as a wholesome corrective to laboratory botany, lies precisely in this.

At the same time any considerable source of new morphological data by which laboratory botany can perhaps in its turn act as a wholesome corrective to pure taxonomy is important, and this is the present significance of cytology. Accurate chromosome counts on a sufficient scale for taxonomic purposes began[2] to become available for the European flora in 1950 (Manton) by the application of newer technical methods than those previously available to fern cytologists. At that time there were only about 100 worked species in at most 23 genera. Discussion of pure taxonomy had in consequence to be limited to problems at the specific level, since problems of genera could scarcely even be formulated in the absence of data regarding families. The very rapid extension of observation since 1950 to the fern floras of several tropical countries, notably Ceylon, Malaya and Africa, with the beginnings of work further afield by other investigators in New Zealand, North America, India and Japan, has begun to rectify this (for more detailed citation see appendix I). We now have information on over 100 genera and 600–700 species, and, although the specific representation is still only about 5 per cent. of those known for the world as a whole, the generic representation is now for the first time reasonably adequate for at least a preliminary characterization of families. The first attempt to do this (Manton & Sledge, 1954) at once revealed inconsistencies in each of the new taxonomic schemes, and in certain cases an unambiguous decision in favour of one out of two otherwise alternative views was possible. It was also possible to pin-point weaknesses and to direct attention to genera of critical importance if further collecting could be done.

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[2] With the sole exception of *Osmunda regalis* L. (Guinard, 1898, for full citation of other literature see Manton, 1939*b*, p. 182) precise accuracy in chromosome counting was not achieved for any fern before 1950, and accuracy to within one or two chromosomes was only reached in a very few cases, notably some counts by de Litardière, 1920 ; Döpp, 1932, 1939 for various species of *Dryopteris* ; Manton, 1939*a* for *D. filix-mas* (L.) Schott and relatives. Even the last two investigators could not, at the dates specified, determine the monoploid number for *Dryopteris* with complete certainty, and it was only finally settled by the use of the acetocarmine squash methods in Manton, 1950.

That such further collecting cannot always be done to order is due in part to a tendency for critically important genera to be thinly scattered over different parts of the world which cannot all be visited. A contributing difficulty has, however, also been a general ignorance on the part of potential collectors concerning what is required and what is possible. A word of advice may therefore perhaps be permitted.

Advice to collectors.

Briefly, what is possible is that almost any fern (with a few outstanding exceptions such as all members of the Ophioglossaceae) can potentially be raised from spores if these are ripe when gathered and protected from undue heat and from sterilization by liquid disinfectants. The spores of many species remain viable for several years (with a few outstanding exceptions such as those of the Osmundaceae which die after a few week's storage). The raising of adult plants from spores, is however, always slow, skilled, and space absorbing if it is to be done on a large scale ; this method is therefore only really useful for special problems or for material from very remote areas. A better way is either to work directly in the field, though this requires experience and training, or else to bring wild specimens into temporary or permanent culture by transplanting. This is less difficult than might be thought for all but a limited category of species. In my experience tropical filmy ferns and the smaller epiphytes can rarely be transplanted, although they may continue to grow for several weeks after gathering if kept moist, so that, notwithstanding difficulty of culture the filmy ferns in particular make excellent cytological material. A limited number of terrestrial ferns will transplant only in an intact sod with the rhizome undisturbed ; this is conspicuously so with members of the Ophioglossaceae. Most ordinary terrestrial ferns will, however, transplant perfectly well, if the rhizome is protected from dessication. This can conveniently be done in polythene or waxed paper bags in which even the most structurally delicate tropical ferns can be safely transported over very great distances. I have in cultivation in Leeds species which originated from Australia or Nepal, sometimes several days porterage away from the nearest airfield, and there are literally hundreds of tropical species in cultivation in London which have been collected in the field by myself, my colleagues or correspondents, and dispatched to England as air freight. Such plants may not immediately or ever develop into elegant specimens suitable for display, but, if reproductively mature when gathered, they may give rise to sporangial material suitable for fixation within a few weeks, if replanted under proper conditions, and since a row of such specimens, each a different individual, need take up no more space than a row of young sporelings pricked out from a single spore sowing, this method of cytological sampling is a highly efficient one given horticultural co-operation at the receiving end and adequate documentation and packing by the sender.

Horticultural material which has been so long in cultivation that details of its original provenance have been lost should be avoided; this rules out almost the entire contents of most botanic gardens. The naming of specimens is a major problem for which the expert services of a good herbarium are indispensable; but no herbarium at present can give more than a more or less rough approximation to the identification of fern material of unknown origin in an artificial habitat.

Given a source of wild material of known origin, a collector who may wish to carry out the cytology himself may reasonably expect to become skilled, with a little practice, (for technical details see appendices to Manton 1950) since complex laboratory equipment is at no point essential. Meticulous documentation is, however, necessary in several ways. At the cytological end there is no substitute for the making of permanent preparations which at need can be submitted to an external critic if doubts arise. At the nomenclatural end there is no substitute for the herbarium record of the actual plant used, amplified with suitable annotations about habitat and locality. Given these, an amateur, resident in a floristically interesting area, can do work at least as good as that of a professional who may be tied up with his profession in a town, though nomenclatural revision will almost always have to be entrusted to a professional. It must not, however, be supposed that attention should in the first instance, or preferably, be devoted to rare or peculiar species. Some of these will almost certainly be encountered if work is done on a sufficient scale, but at least as important, and in the first instance far easier, is the systematic sampling of every different type of species characteristic of a given area including the commonest. If such work can be done in collaboration with a pure systematist interested in the preparation of a revised flora the advantage to both is immediate, and since there its no local flora, especially in the tropics, which is not in constant need of revision there is no limit to the scale of work which is profitable.

Cytology and Status of genera associated with Pteris.

Turning now to " Pteridaceae," we find a potential family which is more controversial than any other of those recently carved out of the " Polypodiaceae of authors " and for which cytology is therefore specially relevant. The following account is still only an interim report. Knowledge has nevertheless substantially increased since the subject was last discussed (Manton & Sledge 1954) and it will perhaps not be out of place to bring together at this time recent observations by other investigators, foremost of whom is Brownlie on the flora of New Zealand, together with published and unpublished records of my own on the floras of Ceylon, Malaya, Africa and Australia to serve as a guide and perhaps a stimulus to the further collecting which is still required.

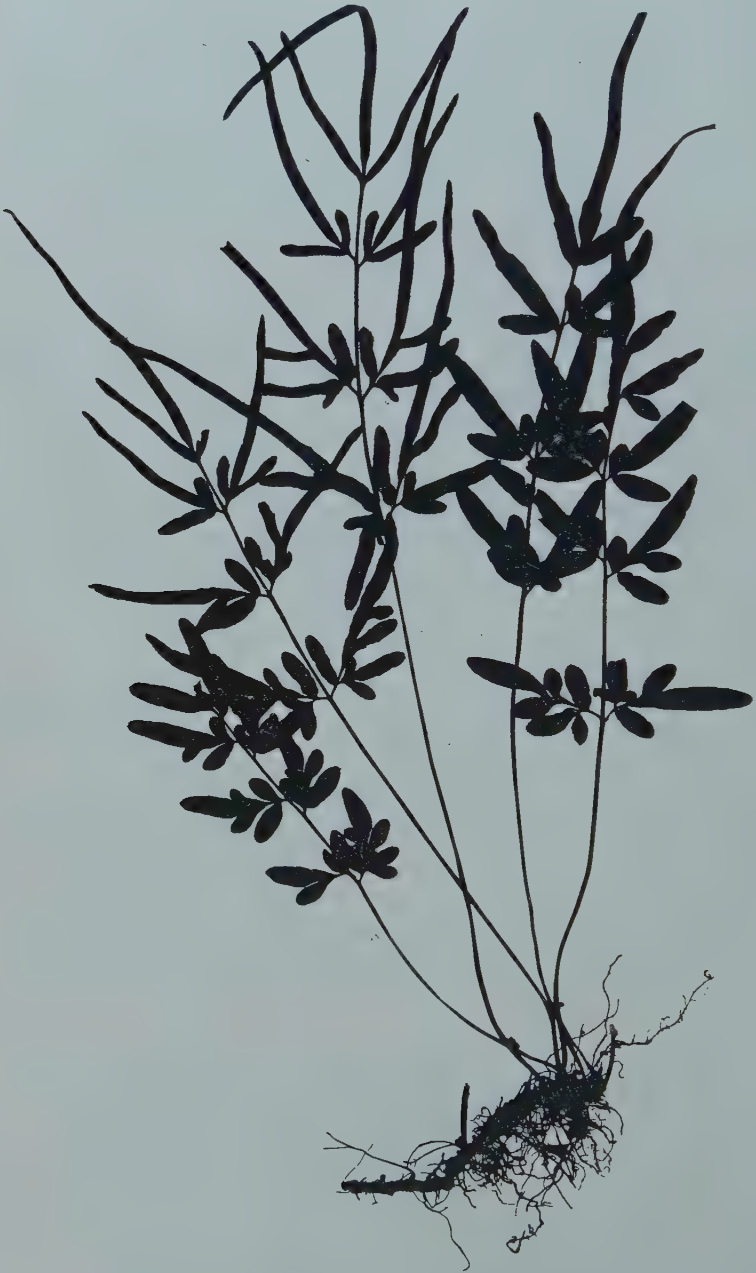
We may start with the genus *Pteris* L. For this, only one species had been accurately, if incompletely, investigated in 1950 namely the apogamous *Pteris cretica* L. The existence of apogamy in it (de Bary, 1878) and of polyploidy (de Litardière, 1920) had already been well established, but the first exact count of $2n = 58$ dates from Manton, 1950. This was demonstrated in a wild European diploid, while approximately twice this number was found in a wild tetraploid plant from Africa. The existence of triploid horticultural varieties, at least one of which was believed to have come originally from a wild source in the oriental tropics, was also confirmed. The meiotic count of 58 in the apogamous diploid was the lowest number actually obtained, since, in an apogamous species, the normal nuclear cycle is eliminated from the life history. It suggested that a basic number in the genus was likely to be 29, though this number was not actually demonstrated for any species of *Pteris* until the work was extended to Ceylon (cf. Pl. 4, fig. 12).

This occurred in the winter of 1950–51 when, during the University Christmas vacation, three members of the staff of the Botany Department at Leeds University visited the island to assemble material for an intensive cytological sampling. No specimens of *P. cretica* were found, and we have reason to think that it is probably now extinct there, although its former presence is attested by specimens. Several other species of *Pteris* were, however, found in abundance and, in particular, the bewildering polymorphism of one most conspicuous population forced us to multiply samples on a considerable scale in order to include a range of forms all falling more or less into the general description of *P. quadriaurita* var. *ludens* of Beddome (1883), though with every possible degree of departure therefrom. A preliminary report on this material was included in Manton & Sledge (1954), together with a photographic demonstration of the expected monoploid number 29, but the full working out was entrusted to the very able hands of my student Trevor Walker who, after a prolonged experimental study which included a visit to Ceylon for field work and further collecting as well as an intensive breeding programme, was able to unravel this problem.

It appeared (cf. Walker, T., 1957, in the press) that *P. quadriaurita* var. *ludens* or its older synonym *P. otaria* Bedd. (Text-fig. 4) is not a species but a morphologically distinctive heterozygote. It cannot breed true, but constantly reappears in the hybrid swarms which develop in abundance when two morphologically very distinct ecospecies are brought into contact by human disturbance to their habitats. Such hybrid swarms are very vigorous and fertile, but show if fully sampled an almost complete range of types bridging the extremes of the parental species. One of the parental species is *P. multiaurita* Ag. (Text-fig. 2), with simply pinnate fertile fronds bearing a certain resemblance to those of *P. cretica*, though the sterile and juvenile fronds are very different. In this, however, *P. multiaurita* bears a close superficial resemblance to *P. ensiformis* Burm. (Text-fig. 1), a very widespread species also present in Ceylon but tetraploid. When first found these two were indeed expected to be linked together (cf. Manton, 1953) in a part parental relationship, an expectation which the breeding work has shown to be entirely unfounded. The other species involved in the hybrid swarms had not, however, at that time been encountered and it was only found by Dr. Walker after analysis of its probable characters as shown by segregating populations raised in cultivation had been completed. It turned out to be a fully bipinnate species (Text-fig. 3), present in pure stands only in secluded areas of primeval forest, and, by means of it, hybrid populations indistinguishable from the wild ones have been synthesized.

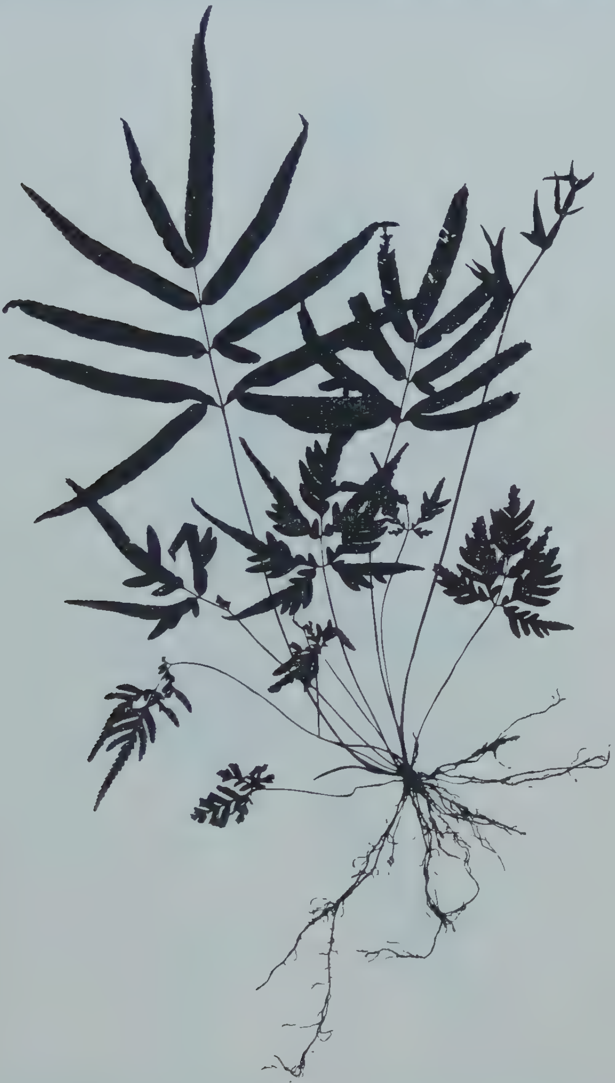
The naming of the second species (Text-fig. 3) was troublesome but proved to be very rewarding. After much expert taxonomic help from the British Museum (Natural History) a type specimen gathered in Ceylon was borrowed from the University Museum in Lund which agreed perfectly. It was the type of *P. quadriaurita* Retz., a geographically restricted species otherwise only known from the Nilghiris in southern India.

The removal of one bad taxon and the clarification of a good one has, however, had the curious consequence of revealing a major confusion not only in Ceylon but in many very widespread tropical areas. There are several other taxa in Ceylon itself some of which are apogamous and which have bred with members of the hybrid swarms. Their influence has now for the first time become recognizable. Further afield, however, the previous unclarity of the situation regarding the behaviour of the species in the type area has led to the placing of almost any, often only approximately similar, specimen from another country into a herbarium cover labelled "*P. quadriaurita* Retz." as if it were a convenient portmanteau. We have received samples of such plants from Australia and Africa which, when grown side by side with those from Ceylon, have shown themselves to be completely different. In the light of Dr. Walker's work the continued use of the name *P. quadriaurita* in any sense other than that appropriate to the south Indian region is no longer permissible, and the true specific composition and naming of the *Pteris* populations of other areas must be worked out afresh. This process need not in each case entail an investigation as



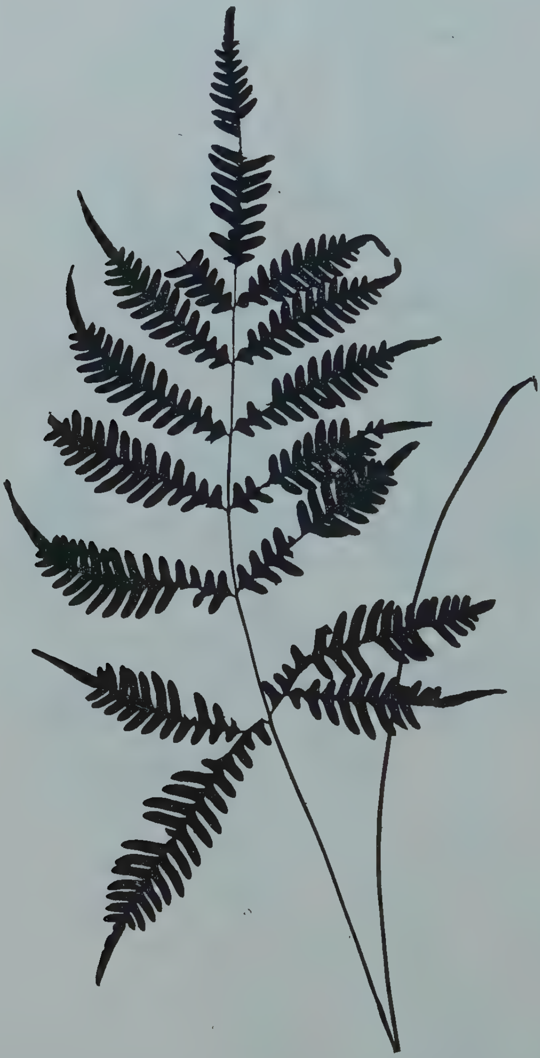
TEXT-FIG. 1.—Complete plant with sterile and fertile leaves of *Pteris ensiformis* Burm. from Ceylon, genetically quite distinct from *P. multiaurita* (Text-fig. 2) which it superficially resembles. $\frac{2}{5}$ths × nat. size.

elaborate as that required for the first clarification. The results already obtained may nevertheless serve as a wholesome reminder of the type of contribution which experimental work can provide, and of the type of situation which cannot in the first instance be adequately understood at all by a herbarium botanist unaided.



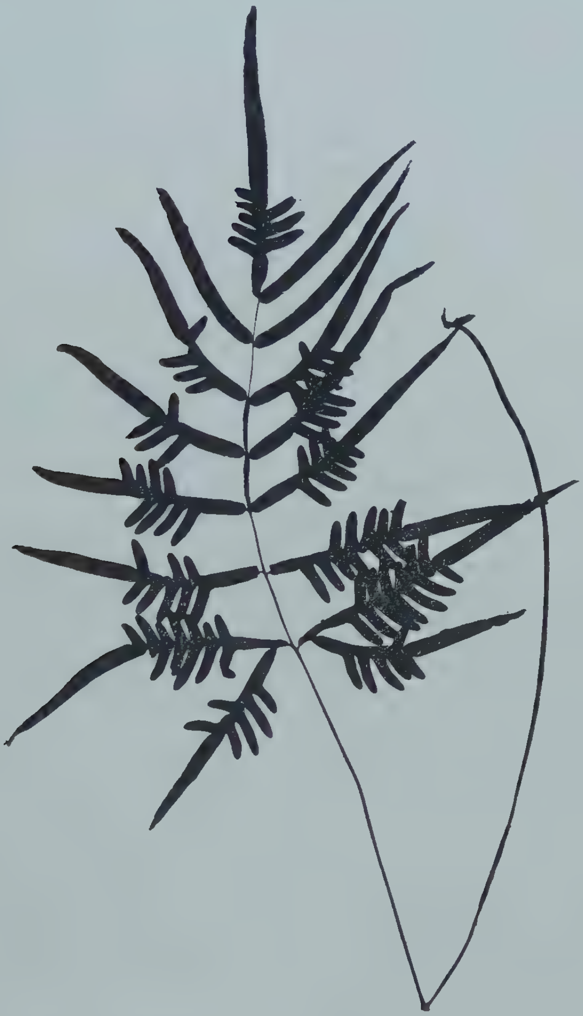
TEXT-FIG. 2.—Complete plant with juvenile and fertile leaves of *Pteris multiaurita* Agard from Ceylon, a diploid superficially resembling the tetraploid species of Text-fig. 1 but unrelated. $\frac{2}{5}$ths × nat. size.

As an example of another type of problem still within *Pteris*, we may conveniently discuss a rare species thought to be related to *P. cretica* by Hooker and others and which we were for this reason specially anxious to investigate as a possible sexual or ancestral type of that species, namely *P. hookeriana* Ag. We failed to establish it in 1950–51, but two specimens were safely transplanted by Dr. Sledge and Dr. Walker on the second expedition in 1953. They proved difficult to cultivate, and were lost after two years, but not before fertile fronds had grown up. When sporangia from these fronds were fixed, they were, very surprisingly, seen to be not quite marginal in position. Since a truly marginal sorus is by definition one of the most essential generic criteria for *Pteris,* we were not surprised to find further discrepancies in spore and prothallial characters, as well as in the chromosome number which proved to be 27 and not 29. To cut a long story short it became evident that, in spite of the earlier convictions of taxonomists as distinguished as Hooker, *P. hookeriana* was not the relative of *P. cretica* that we were hoping to find, but a plant which could only have been included in the genus *Pteris* by mistake. The new generic name of *Idiopteris* has been suggested for it (Walker, 1957*a*, in the press).



TEXT-FIG. 3.—Fertile frond from a wild plant of *Pteris quadriaurita* Retz. from Ceylon, apparently very different from *P. multiaurita* of Text-fig. 2 but actually closely related to it and able to hybridize freely in nature. ⅓rd × nat. size.

The next considerable contribution has come from the flora of tropical Africa. Among the 100 species assembled by post from correspondents, to provide material for an appendix to the forthcoming revised edition of the flora, there are 12 representatives of *Pteris*, some apogamous and some sexual, but all agreeing in possessing $n = 29$ or its multiples. One only need be mentioned. This was sent from the Gold Coast under the well-known name of *P. tripartita* Sw. and it also has $n = 29$. *P. tripartita* in botanic gardens is, however, enormous with 6-ft. fronds far larger than this one. Large plants of this type occur in the Malay Peninsula, and some have been raised from spores collected in that region by Professor Holttum. All are tetraploid. This time it looks as though we probably have, in the Gold Coast, stumbled upon a genuine



TEXT-FIG. 4.—Fertile frond from a hybrid swarm in Ceylon involving the two species represented in Text-figs 2 and 3 showing the intermediate frond shape to which the varietal name of *ludens* or the specific name of *P. otaria* had been given previously (cf. Walker, T., 1957*b*). ⅓rd × nat. size.

ancestral type for a well-known species, though further analysis leading to eventual re-synthesis is still needed.

In addition, however, the African flora produced four species of an entirely different sort which raise at once some far reaching phyletic questions transcending those of mere species. Copeland, in his discussion of the genus *Pteris* gives a careful explanation of his reasons for including in it elements formerly generically separated under the names of *Lonchitis* L. and *Anisosorus* Trev. From Africa I have received one *Anisosorus* and four species of *Lonchitis*. All are cytologically so completely different from ordinary *Pteris*, for which, through Dr. Walker's work, we now have records of over 60 species from four continents, that one is forced to conclude that in this case Copeland was mistaken. *Anisosorus* has not 29 but approximately 50 chromosomes (Pl. 4, fig. 14), while all four species of *Lonchitis* have 38 (Pl. 4, fig. 13), or a multiple, and the chromosomes are larger.

It would therefore appear that, even from our present limited knowledge, the genus *Pteris*, type genus of the Pteridaceae, must be broken up into four unrelated elements, and there may be others. The inclusion of *Idiopteris* was probably accidental. The inclusion of *Anisosorus* and *Lonchitis* on the other hand means nothing less, in the light of the new facts, than inadequacy in the generic diagnosis for the detection of convergent evolution, as discussed on p. 74. Emendation, involving amplification by additional characters is therefore necessary, and, though the cytology is in itself an awkward character to suggest for such a purpose, it can nevertheless perhaps serve as a guide as to where the natural boundaries of the genera may lie.

A situation of this kind in the type genus of a family is likely to be associated with a comparable degree of confusion regarding the family itself. This is indeed what we find, though the fact that the problem of family boundaries is exceptionally difficult for the Pteridaceae is not at once revealed by comparative perusal of our three new systems because each has adopted a rather different attitude to all families which may at first somewhat mask any special circumstances peculiar to one. Ching for example prefers small families, and has in consequence no less than eleven containing only one genus. It is therefore in character that his Pteridaceae should be small and restricted to nine genera of which *Histiopteris* (Agardh) J. Smith, *Pteridium* Scopoli *Pteris* and *Actiniopteris* Link are probably the most important in the present context. Copeland (1947) is at the other extreme, grouping no less than four of Ching's families into his Pteridaceae, which in consequence contains 66 genera, beginning with *Thyrsopteris* Kunze and *Dicksonia* L'Herit. (tree ferns) and ending with *Adiantum* L. all of which are placed in different families by Ching. Holttum on the other hand has dispensed with a Pteridaceae altogether. He accepts Adiantaceae, without defining it in detail, since he is here apparently following Bower, but he tends otherwise to subdivide even more finely than Ching into small groups of genera of less than family status, which he designates by the suffix *-oideae*,[3] and a very varied assemblage of these, including Pteroids, Lindsayoids, Davallioids, Dryopteroids, Asplenioids, etc., are regarded as end-products of divergent evolution radiating from ancestral types near to the present *Dennstaedtia* Bernh. and therefore all to be included in a large family the Dennstaedtiaceae. This view is important in itself, though we need not yet discuss it except to point out that the special ancestral significance attached to *Dennstaedtia* by Holttum should prepare us for finding perhaps certain peculiarities about any family or group of related genera containing it if these are compared with other groups of comparable size but without this suggestion of antiquity.

Returning now to *Pteris*: if we examine the table of contents to Copeland's *Genera Filicum* (1947), which provides a conveniently numbered list of genera within families, we find *Pteris* entered as No. 31 among the 63 genera of the Pteridaceae. Slightly less than half of these genera have so far been sampled cytologically but even with this partial knowledge a somewhat unexpected range and distribution of chromosome numbers has been found, the most outstanding feature of which is that starting with genus 31 (i.e. *Pteris*) there is almost complete cytological discontinuity between the genera above it and those placed below it. The number 29, which characterizes *Pteris* after removal of extraneous elements, is found to be shared by all except one of the sampled genera following *Pteris* in the list except that the variant $n = 30$ occurs concurrently with 29 in several cases (*Aleuritopteris* Fée, *Cheilanthes* Sw. and *Adiantum*), or replaces it in others. The list is as follows, the numbering from Copeland's Index being added as a guide to the assessment of omissions.

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[3] It should be noted that this terminology was also used by Christensen (1938) who erected no actual families within the Polypodiaceae of authors but only sub-families. Christensen's subfamily Pteridoideae contained 12 genera, in substantial agreement with Holttum who follows him in having no Pteridaceae.

TABLE I.—Summary of cytologically investigated genera from the second half of Copeland's Pteridaceae.

Copeland's Index	Genus	Chromosomes	Authority
31	*Pteris* L.	$n = 29$ and multiples	M. & S., 1954; Walker, T., 1957, 1957*a*.
36	*Coniogramme* Fée	$n = 30$ and multiples	M. & S. 1954.
38	*Acrostichum* L.	$n = 30$	,, ,,
39	*Cheilanthes* Swartz	$n = 29$ and 30 and multiples	
41	*Aleuritopteris* Fée	$n = 29$ and 30 and multiples	M. & S., 1954; Panigrahi & M., 1957, in the press.
45	*Pellaea* Link	$n = 29$ and multiples	M. & S., 1954, M., 1950.
47	*Doryopteris* J. Smith	$n = 30$	M. & S., 1954.
49	*Actiniopteris* Link	$n =$ multiples of 29	,, ,,
50	*Cryptogramma* R. Brown	$n =$ multiples of 30	M., 1950.
51	*Onychium** Kaulfuss	$n = 29$ and multiples	Mehra & Verma, 1957; M. unpub.
52	*Hemionitis* L.	$n = 30$ and multiples	M. & S., 1954.
55	*Saffordia** Maxon	$n = 29$–30	M. unpub.
57	*Gymnopteris** Bernhardi	$n = 30$	,,
58	*Pityrogramma** Link	$n =$ multiple of 30	M. & S., 1954.
63	*Adiantum* L.	$n = 29$ and 30 and multiples	M. & S., 1954; Britton, 1953.

* Further details in Appendix II.

Among the genera placed before *Pteris* in Copeland's list only one, No. 20 *Syngramma*[4] J. Smith, is based on a monoploid of 29, and here an error of placing may perhaps be suspected. Ching indeed differs from both Copeland and Holttum in separating *Syngramma* from *Taenitis* Wild, which is cytologically quite different (see Table II), and putting it beside *Coniogramme* Fée (see Table I). If this rearrangement were accepted, the cleavage which starts at genus 31 (*Pteris*) would be complete in that all genera based on $n = 29$ or 30 would then be together, though it would leave behind a somewhat heterogeneous assemblage. Table II lists the first half of Copelands Pteridaceae enumerated in precise detail for all species and genera which have so far been examined but excluding *Syngramma*.

A first glance at this list may perhaps give the impression as of a wholely random array of numbers, yet closer inspection will reveal the presence of several characteristic assemblages which may be expected to fall into better defined categories as sampling becomes more complete. For example the addition by Brownlie of one New Zealand species of *Paesia* St. Hil (No. 24) and of several New Zealand species of *Hypolepis*

[4] *Syngramma quinata* (Hk.) Carr. from Malaya has $n = 116$ with no ambiguity in the count (cf. Pl. 3, fig. 7). This number seems only interpretable as that of an octoploid on 29, or possibly an apogamous tetraploid though no test for apogamy has yet been made.

TABLE II.—Summary of cytologically investigated species from the first half of Copeland's Pteridaceae.

Copeland's Index	Species	Chromosomes	Origin	Authority
2	*Dicksonia squarrosa* (Forst.) Sw.	$n = 65$	New Zealand	Brownlie (2).
	D. fibrosa Col.	$n = 65$	,, ,,	,,
	D. arborescens L'Herit.	$n = 65$	Kew (St. Helena)	M., unpub.
4	*Cibotium splendens* (Gand.) Kroyma ex Skottsberg	$n = 68$ Isles)	Kew (Sandwich Isles)	,,
	C. glaucum (Sm.) Hk. et Arn.	$n = 68$	Kew ,,	
5	*Culcita macrocarpa* Presl.*	$n = 66–68$	Azores	,,
8	*Dennstaedtia punctilobula* (Michx.) Moore	$n = 34$	Canada	Britton, 1953.
	D. scabra (Wall.) Moore	$n = 64–65$	Ceylon	M. & S., 1954.
	D. cicutaria (Sw.) Moore	$n = 94$	Kew	,, ,,
9	*Microlepia platyphylla* (Don) J. Sm.	$n = 43$	,,	,, ,,
	M. puberula v.A.v.R.*	$n = 86$	Malaya	M., 1955 and unpub.
	M. speluncae (L.) Moore	$n = 86$	Ceylon	M. & S., 1954.
	M. speluncae (L.) Moore	$n = 129$	Tropical Africa	M., unpub.
12	*Lindsaya linearis* Sw.	$n = 34$	New Zealand	Brownlie (2).
	L. concinna J. Sm.*	$n = 47$	Australia	M., unpub.
	L. parallelogramma v.A.v.R.*	$n = 47$	Malaya	,,
	L. nitida Copel.*	$n = 47$	,,	,,
	L. scandens var. *terrestris* Holtt.*	$n =$ c. 47	,,	,,
	L. pectinata Bb.	$n =$ c. 50 (= c. 47 ?)	,,	M. & S., 1954.
	L. decomposita Wild.	$n =$ c. 50 (= 47 ?) c. 100	,,	,, ,,
	L. cuneata (Forst.) C. Chr.	$n = 41–42$	New Zealand	Brownlie (2) and unpub.
	L. caudata Hk.	$n = 82$	Ceylon	M. & S., 1954.
	L. cultrata (Wild.) Sw.	$n =$ c. 150	,,	,, ,,
14	*Sphenomeris chinensis* Maxon.	$n =$ c. 100 c. 147	,, Malaya	,, ,, ,, ,,
15	*Schizoloma ensifolia* (Sw.) J. Sm.	$n = 88$	Ceylon	,, ,,
	S. tenerum (Dry.) Hollt.*	$n = 88$	,,	M., unpub.
19	*Taenitis blechnoides* (Wild.) Sw.	$n =$ c. 44	Malaya	,,
23	*Hypolepis punctata* (Thbg.) Mett.	$n = 51–53$ $n =$ c. 100	Ceylon Malaya Ceylon	M. & S., 1954. ,, ,, M., unpub.
	H. rugosula J. Sm.	$n = 52$	New Zealand	Brownlie (2).
	H. millefolium Hk.	$n = 52$	,, ,,	,, (3).
	H. tenuifolia (Forst.) Bernh.	$n = 104$	,, ,,	,, (2).
24	*Paesia scaberula* (A. Rich.) Kuhn.	$n = 26$	,, ,,	,, ,,
28	*Pteridium aquilinum* (L.) Kuhn.	$n = 52$	Europe, Ceylon Malaya, N. America New Zealand	M., 1950 ; M. & S., 1954. Britton, 1953 ; Wagner, 1955. Brownlie (2).
29	*Histiopteris incisa* (Thbg.) J. Sm.	$n =$ c. 96	Ceylon	M. & S., 1954.

* Further details in Appendix II.

Bernh. (No. 23), has greatly clarified the interpretation of both *Hypolepis* and *Pteridium* Scopoli, for the last of which the basic count of $n = 52$ has long been known. We can now see clearly that all three genera must be based on 26 (or perhaps 13). At the top of the list we have clear signs of 34 (or possibly 17) as a base number in *Cibotium* Kaulf, perhaps *Culcita* Presl. and parts of *Dennstaedtia* Bernh. and *Lindsaya* Dryander. We have likewise a series of numbers in the middle forties in the genera numbered 9–22, which are not all fully determined but which undoubtedly include $n = 41$ (some species of *Lindsaya*), $n = 43$ (*Microlepia* Presl.), 44 (*Schizoloma* Gaudichaud non sensu Copeland and perhaps *Taenitis* Wild.), 47 (*Lindsaya* in part and perhaps some species of *Dennstaedtia*). Some of these numbers could be primitive though high prime numbers such as 43 and 47 can scarcely be so. The 65 of *Dicksonia* is also unlikely to be primitive though it may perhaps connect on to certain other species of *Dennstaedtia* which are suspected also to possess this number; it is not known elsewhere.

Whether each of these groups of shared numbers represents a separate phyletic line cannot yet be known, though the probability is strong that some of them may be of this nature. It is certain that we need more material to fill in the facts for the unexplored genera and to amplify knowledge of critical or difficult genera which *Lindsaya* and *Dennstaedtia* seem conspicuously to be. Even in the present state of knowledge, however, the striking contrast between the cytological diversity presented by genera 1–30 of Copeland's Pteridaceae compared with the extraordinary uniformity of genera 31–63 seems in itself to be significant. It is exactly the type of difference which we would expect to find between an old group and a younger one and which we do find if we compare almost any other of the segregates from the "Polypodiaceae of authors" with some of the families which are of equal or greater antiquity than that attributed to *Dennstaedtia* and its allies, namely the Schizaeaceae and Gleicheniaceae. In each of these we have very few surviving genera and every genus is cytologically quite unlike another. Thus in the Schizaeaceae we have *Lygodium* Swartz with $n = 29$ and 30[5]; *Anemia* Swartz with $n = 38$[5]; *Schizaea* Smith with $n = 77$ in the only low numbered species of it which has yet been examined (Lovis, 1957). In Gleicheniaceae we have *Dicranopteris*, Bernh. apparently with $n = 39$ in the oriental tropics (M. & S., 1954, Mehra & Singhe, 1956) though this should be further confirmed since my own count refers in detail to only one plant. Another, not yet officially named, species of *Dicranopteris* is reported from Jamaica to have $n = 43$ (Trevor Walker, personal communication). In New Zealand Brownlie has found $n = 20$, exceptionally large, chromosomes in a species of true *Gleichenia* Bernh., while Brownlie and Walker, from opposite ends of the world and unknown to each other have recorded $n = 34$ for two different species of *Sticherus* Presl., one in New Zealand (Brownlie) and the other in Jamaica (Walker, personal communication). Such extreme lack of resemblance between surviving species or genera in a very ancient group which cannot fail to have suffered enormous extinction suggests that we have here only the fragments of a vanished world, and that these, like the islands in an archipelago, are now held together only by their former relation to a sunk continent, the details of which, as it was in its prime, can no longer be reconstructed.

In contrast if we take the Polypodiaceae sens. strict. of Copeland or the Polypodiaceae sens. strictior plus Grammitidaceae of Holttum, or the Aspidiaceae of Copeland after removal from it of the Thelypteridaceae of Holttum and of Ching, or the Davalliaceae, or Aspleniaceae of Copeland we have assemblages which cytologically are exactly as uniform as is the second half of Copeland's Pteridaceae. The full details cannot be quoted here, nor is this necessary, since, in spite of several additional genera now know in each, there is no significant change from the position outlined in Manton & Sledge (1954). The key number for the Polypodiaceae (including Grammitidaceae) is still $n = 37$ with minor divergences to 36 and more rarely 35, the records now representing 22 out of 65 genera. For the Thelypteridaceae we have $n = 36$

[5] M. & S., 1954.

in 6 out of 9 genera with divergence to 35, 34 and a few lower numbers in one genus only (*Thelypteris* Schmidel). In Aspleniaceae we have almost complete uniformity with $n = 36$ in 9 sampled genera out of a total of 12 for the family. The Davalliaceae have 40 and 41, the latter restricted to *Oleandra* Cav. *Nephrolepis* Schott and *Arthropteris*. J Sm. The Aspidiaceae after removal of Thelypteridaceae have characteristically 41 also (found in 17 genera) though a few genera (*Athyrium* Roth., *Tectaria* Cav. and *Quercifilix* Copel.) have 40 and one (*Cystopteris* Bernh.) has 42.

There would therefore be nothing peculiar from a cytological point of view in accepting genera 31–63 of Copeland's Pteridaceae as a separate family to be called perhaps Adiantaceae. Whether it would be possible in practice to construct a definition for such a family by which members of it could be effectively separated from others, needs expert taxonomic advice. It may be that this is impossible except by defining two families (for example an Adiantaceae proper and a Pteridaceae in a new and much restricted sense). A decision about this is a technical matter about which it would be improper for a cytologist to express opinions.

The question of what should appropriately be done with the remainder of Copeland's Pteridaceae can probably not yet be decided, although clearly the name itself could not be retained in the absence of the type genus. It is probable that recognition of more than one family could be suggested, and may be necessary. This need not, however, be done precipitately unless morphological considerations compel it, since, within the requirement that taxonomy should express phylogeny, there is no hard and fast rule to give guidance as to exactly when, during the submergence of a continent, the resulting islands should cease to be treated collectively. It is, however, proper to stress the need for more information, although these genera are exactly the ones which tend to be thinly scattered, difficult to grow or in other ways inaccessible, so that accumulation of sufficient data cannot be expected to be other than slow. A need for revising the genus *Lindsaya* and perhaps eventually for subdividing the genus *Dennstaedtia* can also be pointed out. More generally interesting than this, however, is the strong probability which the cytology has independently brought out that in essence Holttum's basic idea for an ancestral position of the *Dennstaedtia* complex in relation to several independent lines of descent is possibly right.

A word of warning must, however, be added. It has been shown that intensive random sampling of a few contemporary floras can be used to forge a very potent tool for the detection not merely of human mistakes but those more subtle confusions caused by convergent and divergent evolution. Its power should nevertheless not be over-estimated. The extraordinary constancy of basic chromosome numbers through hundeds of species and dozens of genera in many families of ferns is a positive reason for believing that when unexplained discrepancies are encountered they usually denote human errors of judgement for which, on closer inspection, other evidence can generally be found. We must not, however, rule out the possibility, indeed the certainty, that there will sometimes be exceptions. We have incontrovertible evidence that great numerical changes must have taken place in the past,though whether by large or small steps we cannot yet discern, since without such changes the array of different numbers which we actually encounter as characteristic of the various families could never have been developed. Can we therefore be entirely certain that even peculiar numbers such as 41, 37 or 29 may not occasionally be resynthesized ? If they were, cytology, used alone, would be at least as misleading as any other morphological criterion which, in isolation, cannot discriminate between convergence and divergence. This risk is probably not great for the smaller units in the more modern groups, for which there is usually adequate evidence from other sources for effective criticism to be applied. In comparing the larger units, however, we are sampling the remnants of floras of very diverse ages, and the older the group the less useful does cytology become until, in the extremely ancient groups of which only fragments remain, it may fail us entirely.

In the less extreme case, of which the earlier members of Copeland's Pteridaceae are perhaps an example, we may hope that the evidence, though fragmentary, may not yet have been entirely effaced. This is the reason for their exceptional interest, and why it has seemed profitable to draw special attention to them. The cytological evidence, though new, is nevertheless only part of the whole. Recommendations can be made and reasons given for suggested changes, but a final decision of how best to express phylogeny in terms of the taxonomic system can only be made in the light of all the evidence.

Appendix I.

Recent Chromosome Counts in Leptosporangiate Ferns.

The principal sources of information available to me for the purpose of this article are listed below. This list does not claim to be a complete record of the data on the post-1950 literature, since I have limited citation to work which is personally known to me or which is sufficiently clearly authenicated photographically or in other ways to be accepted as probably reliable ; I have, however, also excluded several small publications, both of my own and others, which add too little to the statistical total to justify the space required for quotation in the present context.

In grouping the citations under floras it is impossible to avoid some overlapping in the enumeration of species. The number of genuinely shared species between floras is difficult to assess. There are only two such species between the floras of Britain and Ceylon (*Pteridium aquilinum* and *Adiantum capillus veneris*), but between Britain and North America (cf. Wagner, 1955) there are about a dozen species which bear the same name though several of these are quite certainly taxonomically separable. For the tropical floras the uncertainty regarding the proper use of specific names for populations in geographically distinct areas is at least as great (compare for example the note on *Microlepia speluncae* (L.) Moore in Appendix II). It has therefore seemed impracticable to adjust the published citations to allow for possible repetitions of this kind. The total for species is therefore likely to be too high by a somewhat uncertain amount for which a reasonable allowance might perhaps be of the order of 10 per cent.

The enumeration of cytologically investigated genera (right hand column) is reasonably accurate. It should, however, be noted that it is impossible in practice to follow any one authority regarding what constitutes a genus. The most extreme case is in the Hymenophyllaceae for which the 30 or so investigated species (Europe 3, Manton, 1950 ; Ceylon and Malaya 8, Manton & Sledge, 1954 ; New Zealand 15, Brownlie (1), (2), (3) ; and India 10, Mehra & Singh, 1955) can be allotted to two genera (*Hymenophyllum* L., and *Trichomanes* L.) on the old system, or to ten, if Copeland's subdivisions are followed. In this particular case I have retained the older usage of two genera since the cytological boundaries do not seem to coincide in detail with those of Copeland's genera. In a few other cases genera not recognized by Copeland have been adopted if cytological discontinuities have seemed to require it. Discussion of these individually will be found in the literature cited or in the text of this article.

With regard to families it should be noted that while the list as it stands refers to leptosporangiate ferns as a whole it is not difficult to allow for a few well-established families which are not controversial. If the Osmundaceae, Schizaeaceae, Gleichenicaeae, Matoniaceae and Hymenophyllaceae are removed, their records amount to about 50 species in 12 genera. What remains is the Polypodiaceae of authors.

	Species	Total genera investigated	Genera newly investigated
1. *Exact counts before* 1950 (see p. 74 footnote²)	1	—	1
2. *Published in Manton,* (1950)—			
British flora	47	19	18
European (non-British)	6	—	1
Madeira flora[6]	38	26	—
Non-European wild	8	6	2
Botanic Gardens	2	—	1
3. *Published in Manton & Sledge,* (1954)—			
Ceylon flora	c. 140	67	54
Other sources not repeated elsewhere	c. 18	—	3
Botanic Gardens	8	—	1
4. *Published (Manton) in Holttum,* (1954)—			
Flora of Malaya	100	43	11
5. *Manton unpublished*—			
Flora of Africa	100	30	3
Additions to Ceylon flora	33	—	4
,, ,, Malayan flora	40	—	2
Other wild sources	c. 40	—	4
6. *Published in Britton,* (1953) ; *Wagner* (1), (2), (3) ; *Manton,* (1951); *Manton & Walker,* (1953) etc.—			
North American flora	30–40	15	3
7. *Published in Brownlie* (1), (2), (3)—			
New Zealand flora	78	30	7
8. *Published by Indian workers* (especially Mehra and collaborators)—			
Flora of Himalayas	c. 30	10	3
9. *Studies on single genera*—			
Dryopteris spinulosa complex (S. Walker, 1955 and unpub.)	c. 20	—	—
Shivas, 1955 ; Wagner, etc.			
Shivas, 1955; Wagner, etc.	c. 20	—	—
Pteris and *Idiopteris* (T. Walker, 1957*a*, 1957*b* and unpub.)	c. 60	—	1
Total	819	..	119

APPENDIX II.

Details concerning species and genera included in Tables I and II or individually mentioned in the text against the citation (Manton, unpublished).

Anisosorus occidentalis (Bak.) C. Chr.—Two adult plants sent from the Gold Coast by Dr. C. D. Adams (cf. Adams & Alston, 1955), fertile in culture at Kew. Chromosomes very small and number slightly uncertain but of the order of $n = 49$–50. Plate 4, fig. 14.

Cibotium splendens (Gaudich.) Krajnia ex Skottsb.—Specimen long in cultivation at Kew under the name of *Dicksonia menziesii* Hk. et Bak. and believed to have come from the Sandwich Islands. Very perfect count $n = 68$.

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[6] The Madeira flora was only included in Manton (1950) in summary form and detailed publication of all the worked species has not yet been carried out, though four were individually quoted in Manton (1950) and three others in Manton & Sledge (1954). Among the total of 26 genera 20 are also European. The remaining six have been included among representatives of the other countries listed, except for *Culcita* Presl. which is described here (see Appendix II).

Cibotium glaucum (Sm.) Hk. et Arn.—As the preceding except for name (Pl. 3, fig. 8).

Culcita macrocarpa L'Herit.—Recently collected wild specimen from the Azores fertile at Kew gave the meiotic count. An approximate count from a root tip on a plant of the same species from Madeira suggests uniformity throughout Macaronesia.

Dicksonia arborescens L'Herit.—This, the type species of *Dicksonia*, is endemic to the island of St. Helena : it has long been in cultivation at Kew and is believed to have been introduced by Thomas Frazer in 1825. $n = 65$.

Gymnopteris rufa (L.) Bernh.—This species is native to tropical America but, like several other ferns from the New World, has become established in Ceylon as a weed of tea plantations. Greenhouse cultivation is easy and it makes a fast growing and decorative pot plant. It is very satisfactory cytological material giving clear preparations readily (cf. Plate 4, fig. 10).

Lindsaya spp.—The count of $n = 47$ is very clearly attested in *L. concinna* J. Sm. (Pl. 3, fig. 5) collected wild in Australia by Melville and in several species brought from Malaya by Professor Holttum and identified according to the terminology used in his book (Holttum, 1954). There is no possibility of confusion with the $n = 34$ recorded by Brownlie for *L. linearis* Sw. in New Zealand, and both these numbers must be accepted for the genus as at present constituted. My own earlier records quoted as *c.* 50 and *c.* 100 in *L. pectinata* Bl. and *L. decomposita* Wild. are not necessarily different from 47 and its multiples since at that time there was no accurate knowledge available (Manton & Sledge, 1954), and both these records were rough estimates. The count for *L. cultrata*, however ($n = c.\ 150$) was expressed as " not less than 150 nor more than 160 " (Manton & Sledge, 1954, p. 146). It was based on good material (cf. loc. cit. Plate 5, fig. 42) and I think it unlikely that this could be a multiple of 47. It is therefore probable that some other numbers are present in the genus in addition to those already found.

Lonchitis spp.—These three species are recent African gatherings sent alive to Kew and identified by Mr. A. H. G. Alston of the British Museum. The tetraploid *L. currori* (Hk.) Mett. came from the Gold Coast and the two diploids from the Belgian Congo (cf. Pl. 4, fig. 13).

Microlepia.—The count for *M. puberula* v.A.v.R. as previously published was only approximate since it was based on a wild fixing sent from Malaya by post. Better results have since been obtained on plants raised at Kew from spores sent by Professor Holttum from Malaya at the same time as the previous fixings. The count is now quite certain and the number ($n = 86$) is that of a tetraploid (cf. the Ceylon and Malayan specimens of *M. speluncae*). The African material $n = 129$ (hexaploid) was raised on two different occasions at Kew from spores sent from the Gold Coast and British Cameroons respectively. A consistent cytological difference of this kind between African and Oriental specimens probably indicates the need for nomenclatural revision.

Onychium.—I have examined one species *O. auratum* Kaulf, (*O. siliculosum* (Desv.) C. Chr.) raised at Kew from spores sent from Nepal (Kew reference 306/55). My count ($n = 29$) agrees exactly with that published independently by Mehra & Verma, 1957.

Pityrogramma triangularis.—This Californian species was mentioned but not illustrated in Manton & Sledge, 1954, but owing to a clerical error the count was recorded as $n = 30$ instead of $n = 60$. Pl. 4, fig. 9 is from the original preparation showing an unambiguous count of 60.

Saffordia.—This very rare monotypic genus is cited by Copeland as known from only one collection. Living material of the only species *S. induta* Maxon was received at Kew from a correspondent in Peru in 1956 and one plant was still alive in 1957. Fixations were taken in both years and though the chromosomes are difficult the number is undoubtedly 29–30.

Schizoloma tenerum (Dry.) Holtt.—This species, gathered in Ceylon by T. Walker in 1954 and since in cultivation at Kew, repeats exactly the previous result on the much commoner species *S. ensifolia* (Sw.) J. Sm. both of which have now given preparations of exceptional clarity showing $n = 88$. This number is almost certainly that of a tetraploid on 44 but since 44 has not so far turned up among the species of *Lindsaya* examined, to which genus these two are referred by Copeland, I am retaining the older nomenclature while recognizing that to do so departs from Copeland's conception of the genus *Schizoloma*.

Taenitis blechnoides (Wild.) Sw.—Specimens from Malaya and from Ceylon have been in cultivation at Kew for several years but have only recently become fertile. They are exceptionally difficult cytologically owing to the profusion of paraphyses which cannot be separated from sporangia and which greatly impede squashing. The meiotic count has only been made on material from Malaya though root tips indicate that Ceylon material has the same ploidy. For further discussion see pp. 83 and 85.

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PLATES 3 AND 4

Samples of the cytology of representative genera from the Pteridaceae sensu Copeland. All preparations in permanent aceto-carmine as described in Manton 1950, photographed and reproduced at a magnification of × 1000.

FIG. 5.—*Lindsaya concinna* J. Sm. (Australia), $n = 47$.

FIG. 6.—*Microlepia platyphylla* (Don) J. Sm. (Kew), $n = 43$.

FIG. 7.—*Syngramma quinata* (Hk.) Carr. (Malaya), $n = 116$ after Manton 1954 in Holttum 1954.

FIG. 8.—*Cibotium glaucum* (Sm.) Hk. et Arn. (Kew), $n = 68$.

FIG. 9.—*Pityrogramma triangularis* (Klf.) Maxon (California) $n = 60$.

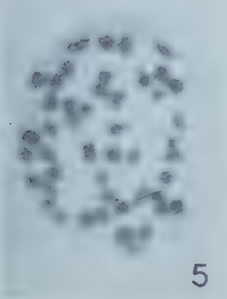
FIG. 10.—*Gymnopteris rufa* (L.) Bernh. (Ceylon, weed), $n = 30$.

FIG. 11.—*Actiniopteris australis* (L.fil) Link (Kenya) $2n = 87$.

FIG. 12.—*Pteris* aff. *quadriaurita* Retz. (Ceylon) $n = 29$ after Manton & Sledge 1954.

FIG. 13.—*Lonchitis mannii* (Gold Coast), $n = 38$.

FIG. 14.—*Anisosorus occidentalis* (Gold Coast) $n = c.50$.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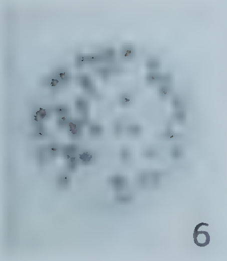
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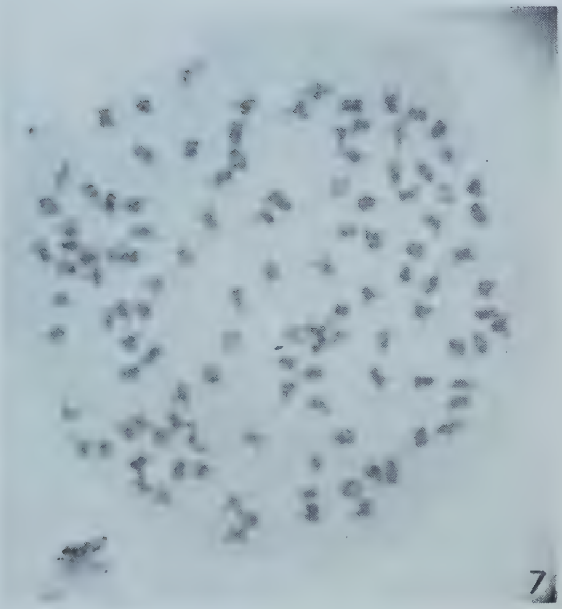
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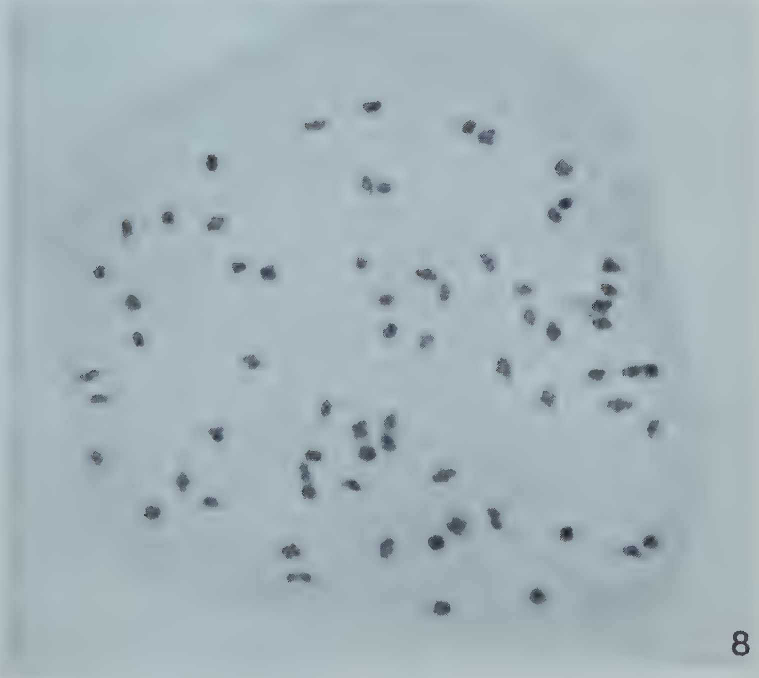
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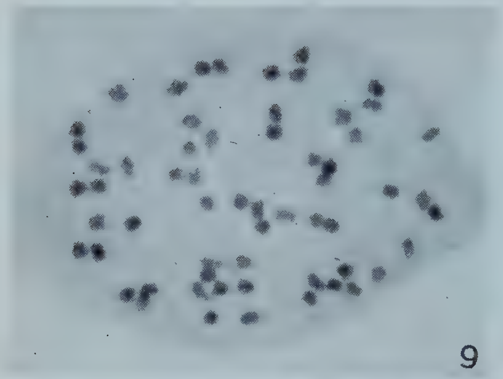
(Description of Plate on p. 92)



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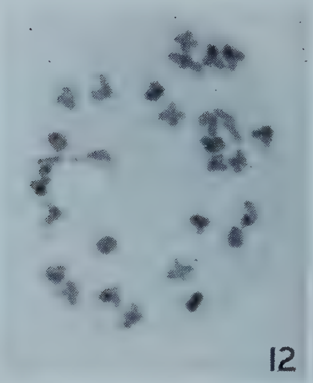

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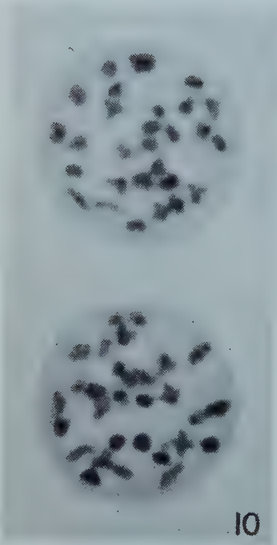

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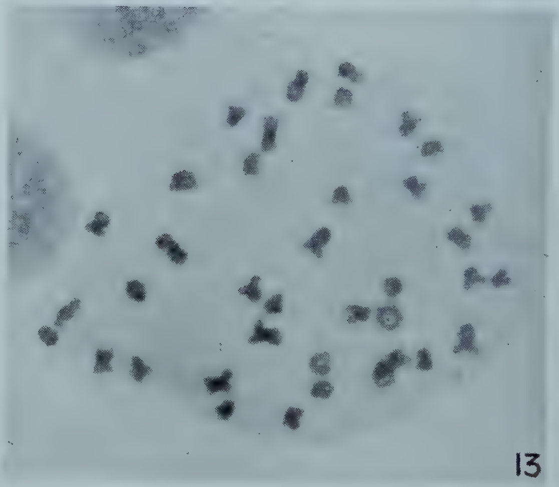

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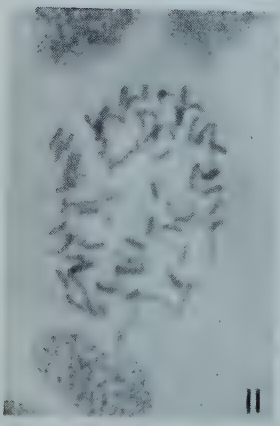

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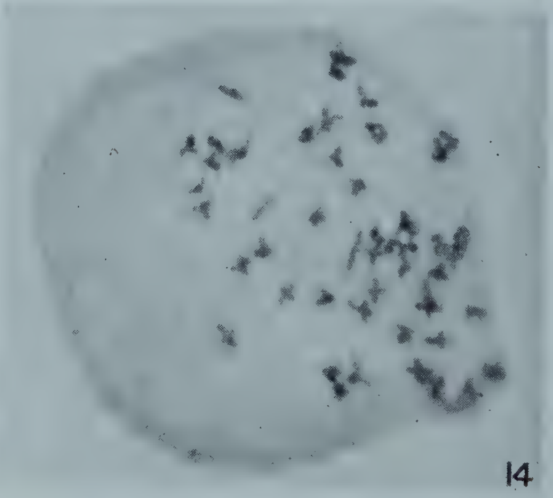

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(Description of Plate on p. 92)

DARWIN, WALLACE, AND "PRE-ADAPTATION"

By L. Harrison Matthews, F.R.S.
Director, Zoological Society of London

New ideas, if they attract wide notice, are often greeted with much hostility; but when their novelty has worn off the hostility may be followed by surprise that such obvious matters had not been discovered long before. Many new ideas, however, are still-born and receive little notice and less acceptance because they are produced to a world that is not ready to receive them—the time is not ripe. The theory of the origin of species by means of natural selection, propounded by Darwin and Wallace in 1858, arrived at a moment when the advancing knowledge of natural history was in dire need of a fertilizer to encourage and direct its growth into profitable channels of investigation. Even more important was their arrival at a time when energetic supporters of new ideas were available to uphold them against the hostility of the orthodox.

Organic evolution was no new idea when Darwin and Wallace put their views forward; indeed, it was a very old one, familiar to the classical philosophers with whom it was summarized in the phrase *πάντα ῥεῖ*. Such concepts were lost to view in the obscurantism of the dark ages, and found no place in the anthropocentric cosmologies of the renaissance which dominated the development of thought until well into the nineteenth century. The increasing knowledge of the natural world, and the application of new scientific discoveries for the material benefit of mankind that came with the birth and growth of modern science gave a feeling of power and confidence that confirmed man's belief in the literal truth of the Holy Scriptures, and his assumption that he was a being apart for whose convenience and use the rest of the universe had been specially created.

During the eighteenth century the rapid exploration of the globe that brought rich spoils from distant regions to the museums, at first private and later public, of all the civilized nations of Europe gave rise to a growing realization of the immense variety in the fauna and flora of the world, a variety almost chaotic until it was reduced to order by the work of Linnaeus. His classification of animals and plants into species and especially into genera implied a kinship between the different kinds of living beings that paved the way for the advancement of the concept of organic evolution. The ground was further cleared by the comparative anatomists and palaeontologists, among whom Cuvier was an outstanding figure, whose work emphasized the similarities as well as the differences between species and larger groups. At the end of the eighteenth century, and in the early years of the nineteenth, many naturalists were thinking about these matters and finding the theory of evolution the only satisfactory explanation of the observed facts. They were much occupied in trying to reconcile the theory of evolution with the observed stability of species. It is surprising, when one considers the number of philosophers, from Goethe and Buffon to Lamarck and Erasmus Darwin, whose attention was focussed on the subject, that an acceptable explanation was so long in appearing.

Although species were known to be stable, it was also known that no two individuals of any species are exactly alike, and that careful examination reveals the existence of numberless minute variations from the average. Variety among domestic animals and plants is conspicuous, and the establishment of the domestic breeds many of which superficially differ from each other as widely as wild species, drew attention to the possibility that some kind of selection analagous to that used by man for improving his domestic breeds might form new species by acting upon the variations found in wild animals and plants.

The natural selection of those individuals most fitted to their environment is almost a truism, especially when expressed in its inverted form as " survival of the fittest ". As early as 1831 the importance of natural selection had been pointed out by Patrick Matthew who wrote: "As the field of existence is limited and preoccupied, it is only the hardier, more robust, better suited to circumstance individuals, who are able to struggle forward to maturity, these inhabiting only the situations to which they have superior adaptation and greater power of occupancy than any other kind ; the weaker and less circumstance-suited being prematurely destroyed. This principle is in constant action ; it regulates the colour, the figure, the capacities and instincts ; those individuals in each species whose colour and covering are best suited to concealment or protection from enemies, or defence from inclemencies or vicissitudes of climate, whose figure is best accommodated to health, strength, defence and support ; whose capacities and instincts can best regulate the physical energies to self-advantage according to circumstances—in such immense waste of primary and youthful life those only come forward to maturity from the strict ordeal by which nature tests their adaptation to her standard of perfection and fitness to continue their kind by reproduction."

It is a matter for wonder that with the theory of evolution or "origin by descent" familiar to naturalists, the obvious fact of the "survival of the fittest" plainly set forth by Matthew, and the well known variability between individuals, the world had to wait so many years for these concepts to be welded into one coherent philosophy. Darwin had indeed arrived at his main conclusions and committed them to writing only eight years after the publication of Patrick Matthew's work. He had, however, communicated them to only a few friends pending the accumulation of the vast mass of supporting evidence that was eventually published in the *Origin of Species*. It was not until the receipt in 1858 of Wallace's essay expounding the same views that Lyell and Hooker insisted on their joint publication in the *Journal of the Linnean Society*.

The Darwin-Wallace communications appeared at the right moment, for the ground was well prepared to receive them. T. H. Huxley tells us that they had the effect upon himself and his contemporaries "of a flash of light, which to a man who has lost himself on a dark night suddenly reveals a road which, whether it takes him straight home or not, certainly goes his way. That which we were looking for, and could not find, was a hypothesis respecting the origin of known organic forms, which assumed the operation of no causes but such as could be proved to be actually at work . . . The "Origin" provided us with the working hypothesis we sought. Moreover, it did the immense service of freeing us for ever from the dilemma—refuse to accept the creation hypothesis, and what have you to propose that can be accepted by any cautious reasoner ? In 1857, I had no answer ready, and I do not think that anyone else had. A year later, we reproached ourselves with dullness for being perplexed with such an enquiry. My reflection, when I first made myself master of the central idea of the "Origin", was, "How extremely stupid not to have thought of that!" . . . The facts of variability, of the struggle for existence, of adaptation to conditions, were notorious enough ; but none of us had suspected that the road to the heart of the species problem lay through them until Darwin and Wallace dispelled the darkness . . ."

As Huxley said, all these things were well known, but their relevance to each other remained unseen until two men at the opposite ends of the earth pointed out how they fitted together. Both men were naturalists who had travelled widely and were familiar with the immense abundance of species, the one particularly impressed by the "family resemblance" between different species inhabiting island groups, and by the extinct forms preserved in the geological record, and the other with the prodigality of tropical nature. Both were influenced, in seeking an explanation of what they had seen, by the writings of Malthus on the growth and natural control of the numbers in human populations. In the first paragraph of his 1858 paper Darwin speaks of the struggle for existence and adds, "It is the doctrine of Malthus applied in most cases with tenfold force". Wallace does not refer to Malthus in his essay, but in his "Life" he tells how when he was at Ternate he "was suffering from a sharp attack of intermittent fever, and every day during the cold and succeeding hot fits had to lie down for several hours, during which time I had nothing to do but to think over any subjects that particularly interested me. One day something brought to my recollection Malthus's *Principles of Population*, which I had read about twelve years before . . .

Then it suddenly flashed upon me that this self-acting process [selection by survival of the fittest] would necessarily improve the race, because in every generation the inferior would inevitably be killed off and the superior would remain—that is, the fittest would survive . . . For the next hour I thought over the deficiencies in the theories of Lamarck and of the author of the "Vestiges", and I saw that my new theory supplemented these views and obviated every important difficulty. I waited anxiously for the termination of my fit so that I might at once make notes for a paper on the subject. The same evening I did this pretty fully, and on the two succeeding evenings wrote it out carefully in order to send it to Darwin by the next post, which would leave in a day or two."

Darwin was thus hustled into the publication of the views he had been developing for twenty years by the arrival of an essay written out in two evenings after being conceived in the fevered brain of his friend sweating in a bout of malaria. Without this stimulus he might well have been another twenty years before publishing—the thoroughness of his methods made his work painfully slow, and his innate modesty made him diffident about publishing. It was only the insistence of Lyell and Hooker that persuaded him into allowing part of his unpublished work to appear with Wallace's essay, and he was fully prepared, and even expressed a wish, to withdraw and allow what honour there may be in priority to fall to Wallace.

The intense hostility and controversy produced by the appearance of the *Origin of Species* a year after the publication of the Darwin–Wallace paper had, fundamentally nothing to do with originality of the ideas put forward by the authors. Their originality lay in proposing a theory that was acceptable to the naturalists of their time as an explanation of the process of evolution; many were already convinced of the fact of evolution, but without a plausible theory to show how it might have taken place they were unable to refute their opponents who held to the doctrine of special creation. They were consequently inclined with Huxley "to say to both Mosaists and Evolutionists, 'a plague on both your houses!' and disposed to turn aside from an interminable and apparently fruitless discussion to labour in the fertile fields of ascertainable fact." When the theory of natural selection made a logical defence of evolution possible the storm broke with a vengeance.

The conflict raged between the Mosaists and the Evolutionists, both of them adhering to beliefs that had been current for several thousand years, but in the confusion and noise of the warring elements the contributions of Darwin and Wallace became distorted. Darwin was credited not only in the popular mind but even in scientific circles with being the originator of the "theory of evolution", a distinction that Darwin never claimed notwithstanding Samuel Butler's spiteful chapter XV on the "Excised My's" in *Luck or Cunning*? The history of that prolonged battle needs no recapitulation; thirty years later Huxley was able to write, "the contrast . . . between the acquiescence, or at least quiescence, of the theologians of the self-respecting order at the present day and the outburst of antagonism on all sides in 1858–59 when the new theory respecting the origin of species first became known to the older generation to which I belong, is so startling that, except for documentary evidence, I should be sometimes inclined to think my memories dreams."

But in 1858 the time was ripe; if Darwin and Wallace had never lived, sooner rather than later someone would have reached conclusions similar to those they published in their Linnean paper; conclusions that would have been generally accepted as valid after a similar heated argument. Huxley writes, "The fact is, that a discerning eye might have seen that some form or other of the doctrine of transmutation was inevitable, from the time when the truth enunciated by William Smith, that successive strata are characterized by different kinds of fossil remains, became a firmly established law of nature." And the ground had been well prepared by Lyell who, paradoxically, had been an opponent of Lamarck's theory of evolution before the publication of the "Origin", and who would have accepted Darwin's theory without reserve if he "could have avoided the inevitable corollary of the pithecoid origin of man—for which, to the end of his life, he entertained a profound antipathy". Speaking of Lyell's *Principles of Geology* Huxley says, " When I consider that this remarkable book had been nearly thirty years in everybody's hands . . . I cannot but believe that Lyell, for others, as for myself, was the chief agent in smoothing the road for Darwin ". By " smoothing the road for Darwin " he appears to mean " preparing the general mental attitude to accept evolution as a fact ", for he says, " The oldest of all philosophies, that of Evolution was bound hand and foot and cast into utter darkness during the millenium of theological scholasticism. But Darwin poured new life-blood into the ancient frame; the bonds burst, and the revivified thought of ancient Greece has proved itself to be a more adequate expression of the universal order of things than any of the schemes which have been accepted by the credulity and welcomed by the superstitition of seventy later generations of men."

Darwin was fortunate not only in his timing of the publication of the *Origin of Species* but also in the presence of champions who were prepared to do battle in defence of his ideas. The publication of the brief Darwin-Wallace paper of 1858, in spite of its modest circulation, was no doubt responsible for the immediate success, from the publisher's point of view, of the " Origin ". Darwin's diary for 1859 notes, " 1250 copies printed. The first edition was published on November 24th, and all copies sold first day ", and later in the year, " During end of November and beginning of December, employed in correcting for second edition of 3000 copies ". One may wonder how the " Origin " would have fared had Huxley not been at hand to fight its battles. Few, even among the scientists, were prepared to speak in its defence—Canon Tristram was the first zoologist to publish his belief in natural selection, " on the strength of the paper in the *Linn. Soc. Journal*, 1858 "—and Huxley remembered none beside himself that was active in its support beyond Asa Gray, Hooker, Lubbock and Lyell who, in spite of his reservations, was " a tower of strength". Darwin was incapable by inclination, apart from his physical weakness, of engaging in controversy, least of all in a heated one, and Wallace " was far away in the Malay Archipelago ". It was Huxley who took up the cause of evolution through the agency of natural selection with the fervour of a religious revivalist, and by his energy and persistence silenced its opponents and obtained the general acceptance of evolution as a fact. Darwin certainly could never have accomplished this; Darwin who "in spite of an acute sensitiveness to praise and blame . . . kept himself clear of all envy, hatred and malice, nor dealt otherwise than fairly and justly with the unfairness and injustice which was showered upon him, while, to the end of his days, he was ready to listen with patience and respect to the most insignificant of reasonable objectors." Nor is it probable that Wallace would have succeeded; it is true that in later years he added much additional support by his writings, but his writing had to be done at leisure away from the heat of argument—he disliked public speaking although he gave many lectures to earn fees—and he confessed that " I am, and always have been, constitutionally lazy,without any of that fiery energy and intense power of work possessed by such men as Huxley and Charles Kingsley."

Neither Darwin nor Wallace had any formal scientific training, and both became involved in the philosophy of biology through an apprenticeship in systematics, Darwin with his *Zoology of the Voyage of the " Beagle "* and his *Monograph on the Cirripedia*, and Wallace through numerous papers describing the birds and insects that he collected in the western and eastern tropics. It is true that Darwin read medicine for two years at Edinburgh before abandoning the subject in disgust and moving to Cambridge to read for the church, but he confesses that his time at the university was entirely wasted and was chiefly devoted to shooting, hunting, riding across country and to collecting beetles merely for the sake of collecting. He was, however, sufficiently interested in natural history to volunteer, at the invitation of Captain Fitz-Roy, as naturalist without pay for the five-year surveying voyage of the " Beagle". Wallace was trained as a land-surveyor and, becoming interested in natural history, collected beetles and butterflies rather more seriously than Darwin. Through his natural history interests he got to know W. H. Bates, and together they planned a natural history collecting trip to the Amazon, the expenses of which they hoped to recover through the sale of duplicate collections. The railway mania of 1846 gave him his opportunity, for he was able to capitalize the trip by saving £100 in six months from the then unheard-of lavish surveyor's pay of two pounds a day and all expenses.

The voyage of the "Beagle", and the first trip to the Amazon, were the turning points in the lives of the two naturalists, and determined the whole course of their future careers on curiously parallel courses, although Darwin was a rich man and Wallace had to earn his living by the constant exercise of his literary abilities almost to the end of his life. Both of them gained an immense knowledge of many branches of natural history, but neither of them was a scientist in the modern meaning of the term. Darwin's methods of patient observation, careful experiment, and deeply pondered conclusion were in the best traditions of scientific thought. Wallace was less self-critical and was very inclined to regard propositions as proved when he had done no more than show that they were probably true. In spite of his brilliant essay of 1858 "On the Tendency of Varieties to depart indefinitely from the Original Type" he came near to letting the trees obscure his view of the wood, for on his return fromMalaya he spent five happy years arranging and describing his collections before he realized that such matters were better left to those more qualified to undertake them. When he turned his attention seriously to the subject of geographical distribution he was able to synthesize his wide knowledge of facts gathered by personal experience into a valuable whole. But he also allowed himself to be diverted, and frittered away his time on such matters as refuting the "flat-earthers", advocating spiritualism and antivaccination, and on many other trivialities, as well as dabbling in theories of socialism and land-nationalization.

It was as philosophers rather than as research scientists that Darwin and Wallace gave an impetus to the study of biology that has lasted a full century, and will continue to stimulate it in the future to an extent that cannot be foreseen. Their ideas, so ably expounded by Huxley, orientated biological investigation in a direction from which it has never seriously deviated, although the main effort of research has from time to time turned into by-roads that have not rejoined the main track for a considerable time, and which indeed for a while appeared to be the main track itself.

Darwin and Wallace were handicapped because the modern science of genetics was not to be born until nearly half a century after the publication of their joint paper in 1858, although breeders of domestic animals and plants had accumulated much empirical knowledge. Without genetics to guide them many of their concepts remained uproven speculations. Wallace tells us that "Darwin always believed in the inheritance of acquired characters, such as the effects of use and disuse of organs and of climate, food, etc., on the individual, as did almost every naturalist, and his theory of pangenesis was invented to explain this among other effects of heredity. I, therefore, accepted pangenesis at first, because I have always felt it a relief (as did Darwin) to have *some* hypothesis, however provisional and improbable, that would serve to explain the facts . . . " Wallace lived long enough to see the theory of the inheritance of acquired characters discredited, and to appreciate from the work of Weismann that changes in inherited characters must be due to changes in the "germ plasm." The discovery of Mendel's work occurred before his death, and although he must have known of it, he evidently did not appreciate its importance to the nascent discipline of genetics, for he makes no reference to it in any of his writings.

Both Darwin and Wallace appear at times to overlook the fact that in dealing with systems of classification the species is the only biological entity, and that genera, families, and the other aggregations of species are merely an expression of the opinion of systematists. When Wallace, for instance, cites the number of genera common to certain islands as evidence of former geographical continuity he deceives himself if he intends to imply more than that the islands are inhabited by species that resemble each other closely. It is impossible to know what he meant precisely, but he gives the impression that he attached more importance and meaning to the word "genus" than is justified. This confusion of thought, if indeed there was confusion, must be attributed. together with his imprecise use of the term "variety", to the contemporary lack of any knowledge of genetics.

Since characters acquired during the lifetime of the individual cannot be inherited, the characters transmitted to the offspring cannot be the result of any direct process of moulding by the environment. New phenotypes must, therefore, be the result of mutation in a gene or genes which chance to meet and produce a homozygous individual unless the gene happens to be dominant. Most of the known mutations are detrimental and the proportion of advantageous ones must be extremely small. Nevertheless, a gene that produces an advantageous character in the phenotype will be likely to spread rapidly through the population in which it occurs if the population is a small one owing to geographical or ecological isolation. A mutation in a gene may, however, produce a phenotype that is at an advantage in a slightly different environment from that hitherto inhabited by the species, so that a new ecological niche can be colonized. Thousands of mutations that are quite useless must occur for every one that confers any advantage. Animals must, therefore, be presented with an enormous mass of potential variation most of which is quickly eliminated by natural selection and only a very small fraction of which is preserved. Time, however, is on the side of advantageous mutations, and when the rare useful ones do turn up the recipients must, if they can, find how to use them to the greatest advantage. So far from the environment moulding the evolution of a species by producing advantageous mutations a species must find the environment in which any new character produced by mutation can be utilized to the best purpose. This process has been loosely and incorrectly termed "pre-adaptation", in the sense that the use for new characters, if they are useful, must be found before they can be preserved by natural selection; "pre-adaptation" taken literally carries an unacceptable teleological implication.

The modern concept of evolution by the cumulative effect of natural selection acting upon random mutations, often individually of small extent, entirely eliminates the Darwinian belief in the inheritance of acquired characters, teleology, Lamarckism, orthogenesis, or any other theory, notwithstanding recent work on genetic assimilation. Random mutations present the possibility of developing new characters for which a use may or may not be found; if they occur at a time when all the circumstances are propitious they may prove to be highly advantageous and lead to profound modifications of structure, physiology, habit or geographical distribution. The essence of the process is the timing of the appearance of the new factor.

By a loose sort of analogy Darwin and Wallace may be said to have been "pre-adapted" when they promulgated their theories. The idea of evolution was thousands of years old, and natural selection or the survival of the fittest was a truism to which attention had already been drawn in the thirties of the nineteenth century, yet they had roused little interest and found no acceptance. It was not until suitable ecological conditions—primarily the intellectual climate—were such that these ideas were adapted to supplant those hitherto current, to survive as the fittest, and to become dominant, that they were more viable than they had been on the previous occasions when they had appeared. One of the most important factors, perhaps the most important, was the presence of Huxley, in the absence of whose energetic support and tireless advocacy and vindication they might well have been ignored for another quarter of a century until the inevitable recombination of circumstances had at last made possible the acceptance of similar ideas produced by their successors. It is ironical that although Darwin and Wallace thought they had discovered how evolution has taken place modern research has shown that their ideas about the inheritance of acquired characters were erroneous, for genetic assimilation has yet to be proved a widespread phenomenon; and that in the popular mind posterity has credited Darwin in particular with originating the "theory" of evolution, a concept that is now accepted as a fact and not as a theory, but which Darwin never claimed as his own.

THE PROBLEM OF THE CLASSIFICATION OF REPTILES

By F. R. Parrington.
(*University Museum of Zoology, Cambridge.*)

(With 7 text-figures and table I.)

The problem.

A view which is maintained by some writers to-day, that all reptiles belong to one of two major taxonomic divisions, had its origin in a paper published by H. F. Osborn in 1903. In this work Osborn claimed that during the previous century too much weight had come to be laid on the manner of fenestration of reptile skulls when discussing the taxonomy of the group, and he emphasized the danger of relying on any such single character. He discussed the outstanding osteological characters, both cranial and post-cranial, of all the principal groups of reptiles then known, and reached the conclusion that each order could be referred to one or other of two great subclasses which he called the Synapsida and Diapsida. These were established on twelve characters which, he believed, were typical but not individually diagnostic. Osborn's grouping of certain orders is plainly erroneous in the light of present knowledge (e.g. he placed the Pelycosauria among the Diapsida), and examination of his characters to-day shows that some were too late in their appearance to be helpful in identifying primitive reptiles, some are of little or no value (e.g. skull proportions), while others have been misunderstood (e.g. the vomers), or must be regarded as having been achieved independently more than once since in certain cases their application is mutually contradictory. But for the most part Osborn's characters are still valid in expressing the great differences which appeared in the course of time between synapsid and diapsid reptiles and, judged from the state of knowledge at the time it was written, his work was a valuable synthesis.

In 1916 Goodrich discussed the matter at some length. He described Osborn's work as epoch-making and accepted his broad conclusions, but he called attention to two characters which he considered had been neglected. The first of these was the " hooking " of the fifth metatarsal which occurs in all modern reptiles in which the foot is properly developed, but which is not known to occur in mammals or in undoubted mammal-like reptiles. Goodrich pointed out that this feature, long known to anatomists, occurred in a very wide range of differently adapted modern reptiles and, implying that it was not, therefore, adaptive, he proceeded to classify those dubious groups in which the structure could be determined according to the presence or absence of this character.

Goodrich then discussed the structure of the heart and the arrangement of the systemic arches in amniotes. He claimed that while the circulatory system of a bird could be derived from that of a modern reptile quite simply, the mammalian system could not. It was therefore necessary to suppose that the earliest amniotes possessed an undivided ventricle and a symmetrical arterial system, not unlike that found in some modern amphibia, to provide a common plan from which both modern reptilian and mammalian circulatory systems could have evolved.

Goodrich suggested that, while it was convenient to retain the class Reptilia, the reptiles should in fact be regarded only as a grade of amniote evolution and he proposed that the amniotes be divided into three groups, the Protosauria, the Sauropsida and the Theropsida. Into the Protosauria, which he regarded as transitional between amphibia and reptiles, he placed the Cotylosauria and the Microsauria (a group of small tetrapods the true nature of which remains uncertain to-day). Into the Sauropsida he placed the typical reptiles and birds, and into the Theropsida the mammal-like reptiles and mammals.

The form of the fifth metatarsal of reptiles has not proved of great value as an indicator of their affinities, and little use has been made of it by subsequent writers, though Goodrich maintained his views when he discussed the matter again in 1942. Here he redescribed the foot of *Youngina*, the oldest ascertainable diapsid, and agreed with Broom that, while the head of the bone was expanded, it could not be regarded as hooked. He agreed also that the foot of *Tangasaurus*, another early reptile believed to be diapsid, showed no hooking of the metatarsal, but dismissed it because it had not been shown beyond doubt to be a diapsid reptile.

The assumption that the hooked metatarsal evolved only once implies the derivation of the Chelonia from diapsid reptiles and this cannot be reconciled with conclusions based on a study of the skeleton in general, which indicates that the Chelonia were evolved directly from the cotylosaurs, possibly the Pareiasauria (Watson, 1914*c* ; Gregory, 1946 ; Olson 1947). It would seem likely that the hooking is a necessary modification following the loss of the fifth distal tarsal and the formation of a mesotarsal hinge, for these two developments are found in typical diapsids but not in synapsids which, while they lose the distal tarsal, form a crurotarsal hinge between the epipodials and the proximal tarsals. It is noteworthy that *Youngina* still retained the distal tarsal, while *Tangasaurus*, which was almost certainly an aquatic diapsid, probably had a webbed foot lacking any marked mesotarsal hinge. Recently Vaughn (1955) has redescribed the foot of the captorhinomorph *Araeoscelis* and shown that, while it has lost the fifth distal tarsal and formed a mesotarsal hinge, it has an unhooked, though widely divergent, fifth metatarsal. But he formed the opinion that the hinge was but poorly developed, the articular surface being " not nearly as well developed as they are in e.g. lizards ".

The assumption that the hooking of the fifth metatarsal was a non-adaptive character of considerable taxonomic value appears to be unjustified. It is likely to have evolved at least twice, and its absence in early reptiles is as likely to be an indication of primitiveness as of relationship.

Goodrich's use of his second character, the nature of the heart and arterial arches, has been criticized by von Hofsten (1941) who pointed out that Goodrich's diagram of the circulatory system of a generalized reptile is misleading and greatly oversimplifies the problem. He called attention to the fact that in the Squamata, Rhynchocephalia and Chelonia, unlike the Crocodilia and birds, blood from the right auricle enters the left side of the ventricle, and that this condition could not well be ancestral to that of the Archosauria. Furthermore he pointed out that the left aortic arch is related differently to the ventricular septum in the Chelonia and the Lepidosauria (Squamata and *Sphenodon*). Von Hofsten's conclusion that, while Goodrich was right in claiming an early separation of the synapsid stock, the heart and systemic arches indicate a splitting of the amniotes into at least four lines of evolution seems eminently correct. Judged from their circulatory systems the reptiles are not diphyletic but polyphyletic.

At about the time of Goodrich's first paper a classification of early reptiles published by Watson (1917) gave promise of support for his ideas, for in it Watson divided the Cotylosauria into three orders :— the Seymouriamorpha, which he regarded as very primitive and are now generally held to be amphibia ; the Captorhinomorpha, which are universally acknowledged to be closely related to the mammal-like reptiles ; and the Diadectomorpha which are not, apparently, so related and can, therefore, be suspected of being related to other reptiles.

In spite of the evidence of Osborn and Goodrich that the reptiles were diphyletic, considerable difficulties remained. Not only were certain small orders too poorly known for them to be referred to one or other subclass with any certainty (e.g.Proganosauria, Protorosauria), but two, if not three, great orders remained isolated because their members showed considerable specializations and no intermediate forms were known which linked them firmly to more primitive orders. Thus both the Ichthyosauria and the Sauropterygia are greatly adapted aquatic animals which lack any clear indications of their ancestry, while the highly specialized Chelonia appear fully developed in the Upper Trias. With regard to the latter Watson (1914*c*) had demonstrated that *Eunotosaurus* from the Permian appeared to link them to the Cotylosauria, but this form (and particularly its skull) is only poorly known, and some writers believe that the Chelonia show diapsid affinities (e.g. de Beer, 1937). In consequence not even Goodrich (1930) himself was later able to classify reptiles according to the views he had expounded.

Meanwhile Williston (1917) had been unable to group the reptiles into fewer than four subclasses. Emphasizing skull structure, he separated the Cotylosauria and Chelonia as the Anapsida, recognized the Synapsida and Diapsida, and added a new subclass, the Parapsida, for the Proganosauria, Protorosauria, Ichthyosauria and Squamata. Later (1925) he removed the Sauropterygia from the Synapsida into a separate subclass, the Synaptosauria. Williston's subclass Parapsida expressed his belief in the origin of lizards from a reptile with a single, upper, temporal vacuity, such as *Araeoscelis*, by emargination of the cheek region from below, but this view was denied by the discovery of *Prolacerta* and *Pricea* which demonstrated the diapsid origin of the group (Parrington, 1935; Broom & Robinson, 1948*b*).

Subsequently Romer (1933, 1956) has adopted somewhat similar classifications, placing the Ichthyosauria and Sauropterygia in separate subclasses (the latter with the Protorosauria) but dividing the diapsid reptiles into two subclasses, the Lepidosauria and the Archosauria.

In spite of the difficulties several writers have recently supported the view that the reptiles are essentially diphyletic. Westoll (1942*a*) called attention to the resemblances of certain of the " microsaur " amphibia (the microbrachiids) to the captorhinomorph cotylosaurs and, while he maintained that the seymouriamorphs, captorhinomorphs and diadectomorphs could be derived ultimately only from anthracosaur-like stegocephalians, he suggested that the differentiation of the primitive reptile stock might have taken place while they were technically still amphibia. Later (1942*b*) he drew attention to the possibility of the cotylosaurs being related to the Microsauria and to the Ichthyostegalia rather than the anthracosaurs.

The next attempt to classify the reptiles diphyletically was made by Olson who, in 1947, gave a revised account of the skull of *Diadectes*. This described for the first time a curious modification of the inner ear resulting in the fenestra ovalis being situated at the end of a long tube formed largely by the opisthotic and parasphenoid bones. Olson pointed out that this specialization closely resembled a similar development in *Seymouria* as described by White (1939) and, since he also believed that *Diadectes* retained an intertemporal bone, and that the pattern of the bones of the temporal region was very similar to that of *Seymouria*, he claimed that the two forms, and so their allies, must be closely related. Olson went on to argue that the Chelonia resembled the Diadectomorpha so closely that their common origin must be accepted, but at the same time he accepted Westoll's suggestion that the Captorhinomorpha showed remarkable resemblances to the microbrachiid Microsauria. He therefore proposed that the class Reptilia be divided into the subclass Parareptilia, comprising the seymouriamorphs, the various diadectomorphs and the Chelonia, and the subclass Eureptilia comprising the captorhinomorphs and all other reptiles. It is noteworthy that this view relates the diapsid reptiles to the synapsid reptiles rather than the diadectomorphs, and also that the common ancestry of the two divisions of the amniotes is to be found only in the primitive embolomerous amphibia. The implication of this interpretation is that those characters which are commonly believed to hold the Amniota together as a group (the amnion and allantois, gastrocentrous vertebrae, the metanephric kidney and ureter) were evolved independently in Chelonia and other reptiles.

Olson's comparison of the middle ears of *Diadectes* and *Seymouria* and his claim that they are related, are accepted by Watson (1954) who, however, denies the presence of the intertemporal bone in *Diadectes*. But the elongation of the perilymphatic duct in these two forms results in a shortening, and so presumably a lightening, of the stapes and, particularly since a similar modification took place in the quite unrelated Dicynodontia, the possiblity of the modification being a result of convergent adaptation is real, and receives support from the fact that, with a partial exception in *Nyctiphruretus*, it does not occur in other diadectomorph reptiles.

The most recent work on the subject has been that of Watson. In 1953 he discussed the evolution of the mammalian middle ear and claimed that the captorhinomorph cotylosaurs, and all synapsid reptiles except the most advanced theriodonts, lacked a tympanum, and that the organization of their middle ears was essentially different from that of modern reptiles. In 1954 he gave an account of the skulls of certain early diadectomorph and captorhinomorph cotylosaurs and claimed that the stapes and quadrate were so different in the two groups that they were diagnostic of the two fundamental divisions of the Amniota except, perhaps, in the, as yet unknown, earliest forms. Quite recently (1957) he has given an acount of *Millerosaurus*, one of a series of small reptiles described by Broom (1938) and Broom & Robinson (1948*a*, 1948*b*) who believed them to be related to the captorhinomorphs and, possibly, the diapsids and certain other reptiles. Watson, however, claims that they are members of Goodrich's " Sauropsida ", and quite unrelated to the Captorhinomorpha, and he has established a case to show that they may well have been ancestral to the diapsid reptiles. And, like Olson, he finds a common stem for the two great divisions of the Amniota only in the early labyrinthodonts.

It will be seen from this account that the evidence which has been used to support the view that reptiles are essentially diphyletic has changed repeatedly since it was first advanced more than half a century ago; that the idea has repeatedly been opposed; and that to-day it rests almost entirely on the interpretation of the middle ear of early reptiles and on the nature of the millerettids.

The Middle Ear of Early Reptiles.

Watson's interpretation of reptilian middle ears starts from the character he used to classify the Cotylosauria in 1917. Here he defined the Diadectomorpha as cotylosaurs with exaggerated, laterally placed otic notches, and the Captorhinomorpha as cotylosaurs without an otic notch, both orders differing from the Seymouriamorpha in having vertically placed quadrates. According to this interpretation the amphibian ancestor of reptiles had a dorsally placed otic notch and a sloping quadrate and the latter became vertical, the better to withstand vertical thrusts, in one of two ways. Either the lower, articular, end moved forwards, allowing the tympanum to move downwards into an enlarged otic notch (Diadectomorpha), or the dorsal end moved backwards, obliterating the otic notch, and with this change the tympanum was lost (Captorhinomorpha). This interpretation was developed and has been maintained in a series of papers on cotylosaurs and on reptilian ears (Watson, 1914*a* and *b*, 1919, 1951, 1954), and has led to the belief that no tympanum was present in synapsid reptiles except in late theriodonts where the mammalian tympanum appeared, held by the angular with its reduced reflected lamina. This interpretation has been supported by the belief that the often massive stapes of such reptiles could not have functioned satisfactorily with the aid of a tympanum, and that they were, in fact, held rigidly. But the work of other palaeontologists is in contradiction with much that is claimed.

A cynodont tympanum of the nature supposed by Watson (1951, 1953) is difficult to reconcile with other data. It is extensive and superficial and would need no external auditory meatus, yet it is universally agreed that the presence of such a structure is indicated by the hollowing of the back of the squamosal. Moreover a soft meatus housed in this structure must be supposed to have left it to reach the outer surface of the tympanum, making a connection with the mobile lower jaw, while the tympanic cavity must be supposed to have led from the inner surface of the tympanum back into what is, in some skulls, a continuous, well-formed, bony funnel in the squamosal, and then medially to enclose the stapes (fig. 1). The alternative interpretation of such animals is to suppose that a tympanum, if present, must have been situated both at the termination of the external auditory meatus and also at the lateral extremity of the stapes, and these two positions coincide to place the tympanum in a position which is essentially reptilian in being postquadrate (Parrington, 1949). This interpretation has the advantage of accounting for the appearance of an external auditory meatus in synapsid reptiles. The assumption of a postquadrate tympanum in primitive pelycosaurs suggests that the development of a meatus in such larger and more specialized forms as *Dimetrodon* resulted from the prolongation of a shallow meatus, consequent upon the increased size and the lowering of the quadrate far below its original position. Such an early appearance of the meatus would account for the hollowing at the back of the squamosal in therapsids generally, a hollowing which cannot reasonably be interpreted in terms of the jaw musculature (Parrington, 1955). Furthermore, this interpretation accounts for the various known stapedial processes in accordance with the broad interpretation of such processes advanced by Westoll (1943). Finally the doubts which have been expressed as to the possibility of large stapes, such as those found among pelycosaurs, being capable of functioning with the aid of a tympanum, appear to have been resolved by the work of Hotton (1956 ; in press), while the suggestion that they were held rigidly is denied by the frequency with which they have been lost.

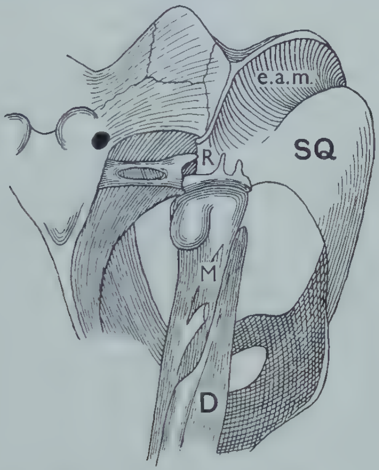
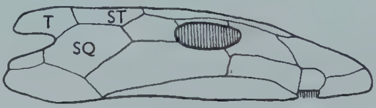


FIG. 1.—The ear region of the cynodont *Diademodon*, drawn from a model, to show the two possible positions of the tympanum. R is the reptilian position at the distal end of the stapes and the termination of the osseous external auditory meatus (*e.a.m.*). M is the mammalian position, the tympanum being held by the angular and its reduced reflected lamina. D, dentary ; SQ, squamosal.

It appears clear that the supposition of a postquadrate tympanum in synapsid reptiles generally must be held to be reasonable and to carry with it the assumption of such a tympanum having been present in their captorhinomorph ancestors. It would appear, therefore, that if in fact the captorhinomorph reptiles were descendants of anthracosaur or seymouriamorph amphibia, the tympanum was not obliterated with the loss of the otic notch but moved ventrally to a postquadrate position. But a consideration of the other groups of early amphibia suggests that this is not, in fact, what occurred.

The tetrapod otic notch is generally accepted as having been derived from the fish spiracular cleft. It has been established in a range of early crossopterygian fishes that the spiracle opened at the anterior part of the contact between the squamosal and the bone now usually identified as the tabular, and that the supratemporal may or may not enter into the formation of the spiracular notch (Jarvik, 1944, 1948). Examination of Carboniferous and later labyrinthodonts shows that the otic notch is formed by the same two bones, the squamosal and tabular, again with the supratemporal forming part of the border in some instances. Since the identification of the labyrinthodont otic notch as such has been established beyond reasonable doubt, the stapes having been found in position in many cases, and being locked in position in those forms having the bone fused to the parafenestral crista, the only reasonable conclusion is that the typical labyrinthodont stapes occupied essentially the same position as the crossopterygian spiracle (fig. 2).



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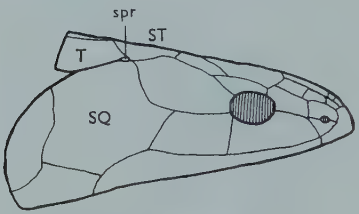
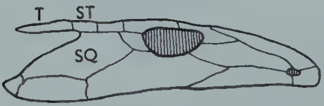


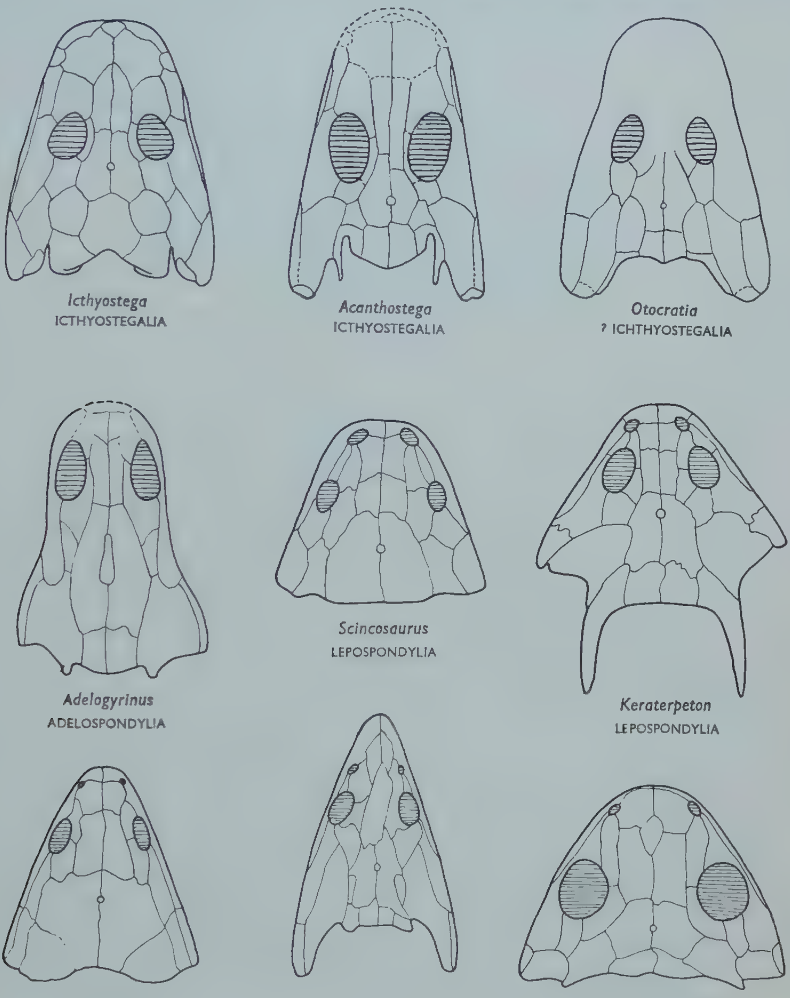
EUSTHENOPTERON



PALAEOGYRINUS

Fig. 2.—The skulls of *Eusthenopteron*, a crossopterygian fish (after Jarvik); *Ichthyostega*, an Upper Devonian amphibian (after Jarvik); and *Palaeogyrinus*, a Carboniferous labyrinthodont (after Watson). The otic notch of the labyrinthodont reaches the position of the fish spiracle (*spr*) at the back of the supratemporal (ST); this region has been closed in the ichthyostegid by the suturing of the tabular (T) and squamosal (SQ).

Among modern amphibia only certain anurans have kept the tympanum and tympanic cavity, and in these rapid metamorphosis obscures the manner of development of the middle ear. But it is known that in the development of reptiles and birds the spiracular slit is closed from below upwards leaving the epibranchial placode in a dorsal position which is held to mark the position of the fish spiracle, while the tympanic cavity arises as a diverticulum from the more ventral region of the gill pouch which expands and forms the tympanum where it becomes applied to the ectoderm (Goodrich, 1930). Since the tympanic cavity and tympanum develop ventrally to the relic of the fish spiracle, their more ventral origin can be expected, and in consequence an old interpretation of the tetrapod middle ear cavity as a derivative of the fish spiracle has been almost entirely abandoned. But the evidence against this view has been derived from a study of amniotes, while a reconsideration of the relevant ossifications in labyrinthodonts appears to support it, and so suggest the possibility that labyrinthodonts differ from the amniotes in at least the position of their tympanic cavities. The classification of the early "stegocephalian" amphibia is contentious, recent classifications tending to place the Upper Devonian Ichthyostegalia as allies of the labyrinthodonts and to group all remaining orders together as the Lepospondylia (Romer, 1947, 1950), the Phyllospondylia being regarded as larval labyrinthodonts (Romer, 1939). An examination of the otic regions of these other stegocephalia shows that while the phyllospondyls resemble the labyrinthodonts the others do not.



Icthyostega
ICTHYOSTEGALIA

Acanthostega
ICTHYOSTEGALIA

Otocratia
? ICHTHYOSTEGALIA

Adelogyrinus
ADELOSPONDYLIA

Scincosaurus
LEPOSPONDYLIA

Keraterpeton
LEPOSPONDYLIA

Michrobrachis
ADELOSPONDYLIA

Urocordylus
LEPOSPONDYLIA

Ricnodon
LEPOSPONDYLIA

FIG. 3.—Devonian and Carboniferous Stegocephalia showing the closure of the spiracular cleft and absence of any conspicuous otic notches. Data from Jarvik, Watson and Steen.

The earliest recorded tetrapods, the Upper Devonian Ichthyostegalia, are known from two rather distinct types. In *Ichthyostega* and *Ichthyostegopsis* there is a distinct "otic notch" formed by the tabular and squamosal bones, but, unlike the condition in the labyrinthodonts, the notch is formed by the posterior parts of these bones and anteriorly, in the region of the fish spiracle, they are joined together by a well formed suture (fig. 3). Such a notch may have been an otic notch, but in the absence of any information about the stapes, it is impossible to be sure that it is not, in fact, merely a relic of the fish spiracular cleft. Moreover in the allied *Acanthostega* (Jarvik, 1952), and in *Otocratia* from the Lower Carboniferous of Scotland (Watson, 1929) the whole of the fish spiracular cleft has been closed, the tabular joining the squamosal far posteriorly, and if any otic notch was present it was formed by the development of a

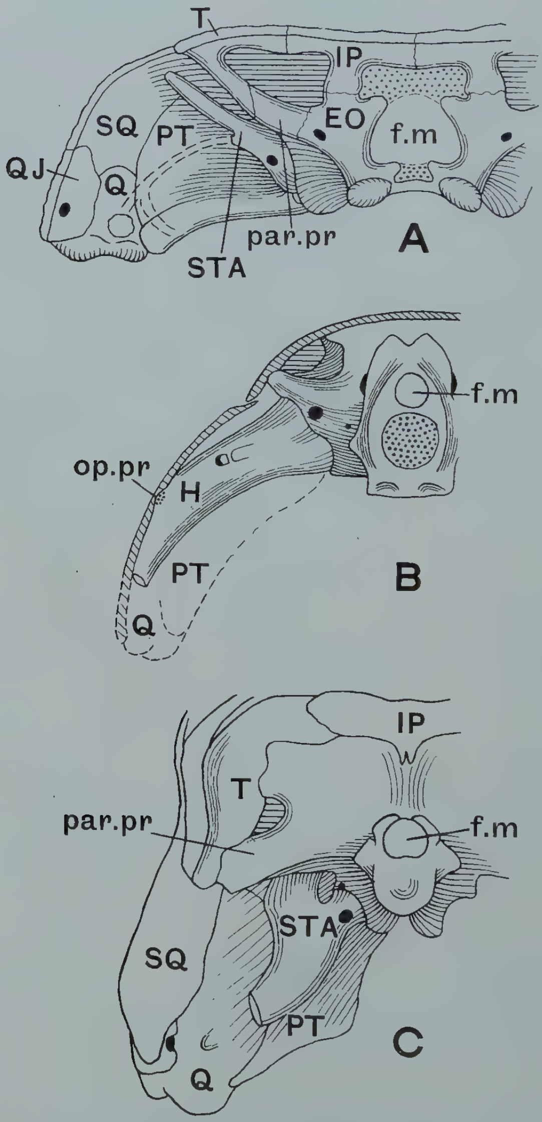


Fig. 4.—Occipital views of the crossopterygian fish *Eusthenopteron* B, the labyrinthodont amphibian *Lydekkerina* A, and the pelycosaurian reptile *Dimetrodon* C, to show the resemblances between the reptilian stapes (STA) and the fish hyomandibular (H). B derived from Jarvik, C from Romer and Price. EO, exoccipital ; IP, interparietal ; PT, pterygoid ; Q, quadrate ; QJ, quadratojugal ; SQ, squamosal ; T, tabular. *f.m.*, foramen magnum ; *op.pr*, opercular process ; *par. pr*, paroccipital process.

tabular horn in *Acanthostega*, or, possibly, it was formed posteriorly to the tabular bone in both cases. Clearly the condition in these Ichthyostegalia is very distinct from that in the labyrinthodonts proper.

A general survey of the remaining groups of early (Carboniferous) amphibia shows that the condition of the posterior part of the skull is very variable, and that in only a few cases is there any evidence which can be interpreted as indicating an otic notch at all. Furthermore, where this exists it appears to indicate that the tympanum, if present, must have been behind the squamosal (fig. 3).

The suggestion that the labyrinthodont and reptile middle ears may have been somewhat different in their manner of development finds support in the relations of the stapes for, as Suskin (1927) pointed out, the substantial, ventrally directed, bone of early reptiles more closely resembles the hyomandibular of early crossopterygian fishes than does the dorsally directed stapes known in labyrinthodonts (fig. 4), and the direct derivation of the reptilian condition from that of the fish, rather than from that of the labyrinthodont amphibian, would be relatively simple.

A well known difference between amphibian and reptilian middle ear structures is found in the course of the chorda tympani, a branch of the facial nerve which in frogs is post-tympanic but which in all amniotes is pre-tympanic. Various attempts have been made to reconcile these differences (Goodrich, 1930), some writers even suggesting that the tympana of the two are not homologous structures, but an interpretation suggested by Westoll (1943) on palaeontological grounds, is of considerable interest in view of the variation found in skull structures of early amphibia. Westoll accepted Eaton's equation of the opercular process of the fish hyomandibular with the extra-stapedial process of the tetrapod stapes, and supposed that the original tetrapod tympanum developed behind the squamosal, but moved dorsally in typical amphibia and ventrally in reptiles. The internal mandibular branch of the facial nerve, which becomes the chorda tympani and in the crossopterygian fish passes through the hyomandibular in a tunnel of some length, escaped ventrally to the critical process when the stapes migrates dorsally, but dorsally when, in reptiles, the stapes moves somewhat ventrally. The neutral position of the early tympanum suggested by this interpretation is in accordance with the evidence provided by non-labyrinthodont amphibian skulls where the spiracular cleft has been closed and the only apparent position of an otic notch is behind the squamosal ; and it allows the reptilian stapes to be derived directly from one in much the same position as a fish hyomandibular.

These conclusions suggest that the primitive reptile skull was one with little evidence of the spiracular cleft or of an otic notch (fig. 5) and so, except for the retention of dorsally situated interparietals and tabulars, might resemble that of the early captorhinomorph *Limnoscelis*. This is in accordance with Romer's conclusions that *Limnoscelis* is the most primitive known reptile and is sufficiently generalized to be regarded as representing the common stem from which all lines of reptiles could have evolved. Furthermore, as Romer pointed out, the condition of the cheek in *Diadectes* with its exaggerated otic notch could easily be derived from that of such a reptile (Romer, 1946). This interpretation would account for the upright quadrates of reptiles as a result of the shortening of the cheek region, a phenomenon of widespread occurrence in vertebrates ; it would account for the resemblance of the reptile stapes to the fish hyomandibular as a result of almost direct derivation ; and it suggests that the typical high position of the labyrinthodont tympanum and stapes was a peculiarity developed within the group and not a condition ancestral to that of the Amniota.

The Relationships of the Millerettids.

In his account of *Milleretta* (*Millerina*) Broom (1938) pointed out certain resemblances between it and *Captorhinus*, though he noted considerable differences in the occiputs ; and then, in an addendum, he emphasized likenesses to the more primitive captorhinomorphs *Romeria* and *Protorothyris* and the primitive pelycosaur *Eothyris*, adding that " the general agreement between *Eothyris* and *Millerina* is remarkable ". But his comparisons were brief and he interpreted the supratemporal and tabular bones together as the tabular. Watson (1957) compared the Millerosauria and early " theropsids ", noting a remarkable similarity in the sutures between the parietals and the frontals and prefrontals (fig. 6) and recognizing identical relations and manner of attachment between the parietal lappet and the supratemporal and squamosal bones holding, however, that the latter similarity was due to common inheritance from anthracosaur ancestors. But he claimed that the millerettid squamosal is in contrast to that of all " theropsids " in capping the quadrate while leaving it entirely

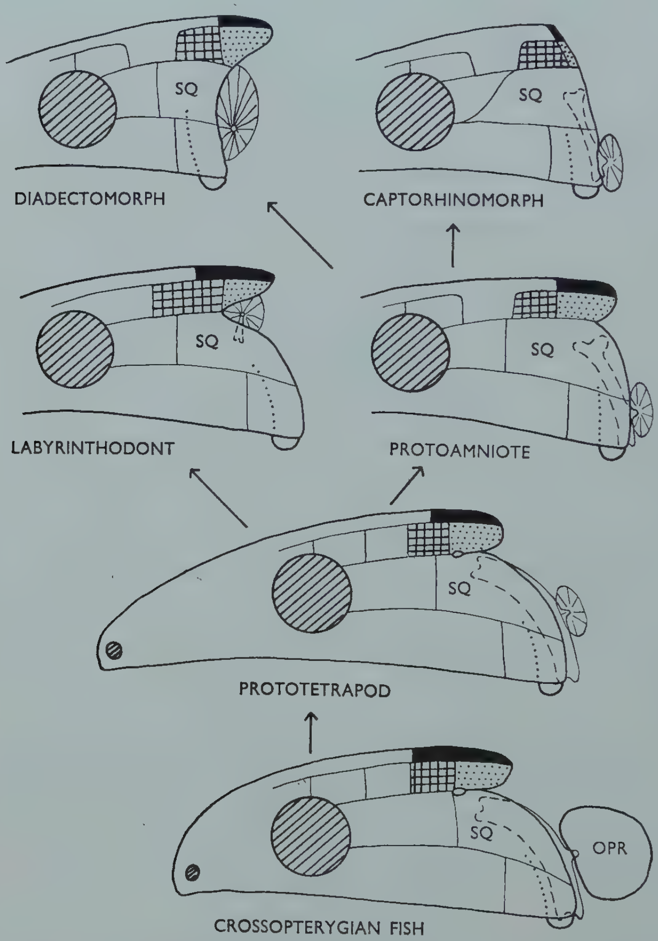


FIG. 5.—Diagram of the suggested manner of evolution of the postorbital region of the tetrapod skull by a shortening of the cheek region, the quadrate becoming more vertical ; the closure of the spiracular cleft, except in the labyrinthodonts ; and the downward movement of the interparietals (black) and tabulars (stippled) on to the occiput in the captorhinomorphs. In the labyrinthodont the region of the missing intertemporal is filled by an anterior growth of the supratemporal (cross hatched) and a posterior growth of the postfrontal ; in the amniotes by a lappet of the parietal. The massive hyomandibular bone of the fish is reduced in size and forms the stapes ; the tympanum develops in the region of the fish opercular and moves progressively forwards with the shortening of the cheek except in the labyrinthodont where it moves up into the spiracular cleft. OPR, opercular ; SQ, squamosal.

exposed posteriorly, and that the millerettid middle ear, with a tympanum situated below the supratemporal and behind the quadrate, was in contrast to the condition in " theropsids " which had, apparently, lost the tympanum, and he concluded that the millerettids were " sauropsids ".

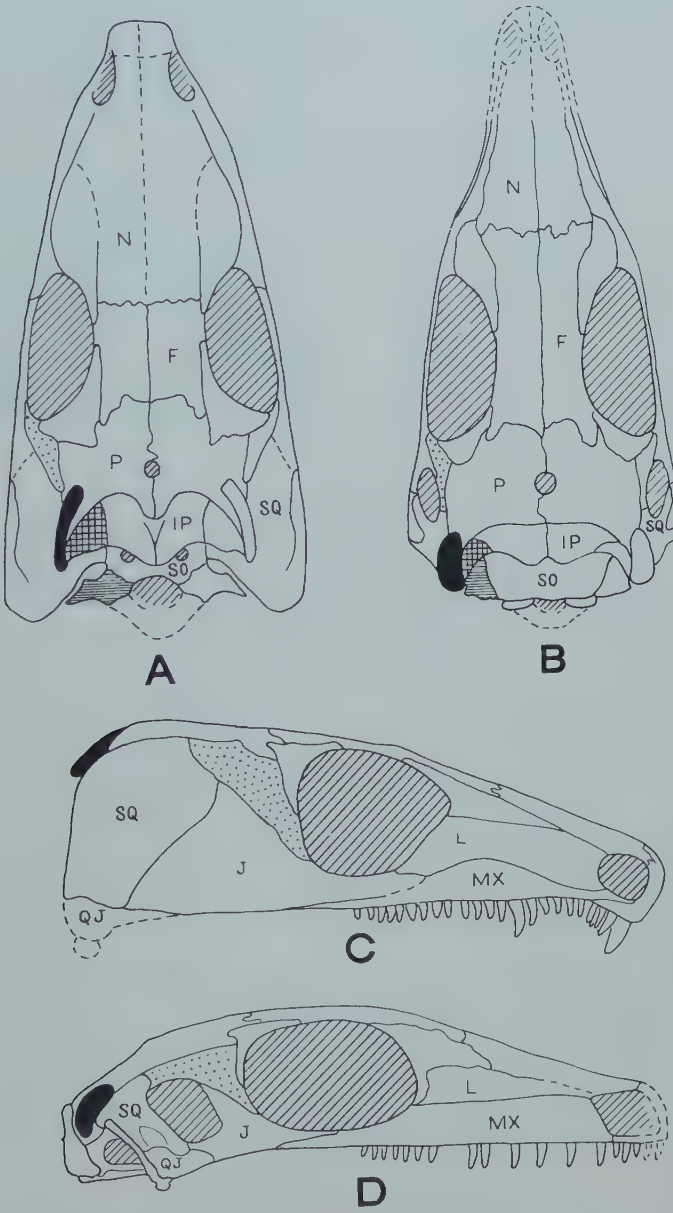


FIG. 6.—The skulls of the captorhinomorph cotylosaurs *Protorothyris* A and *Romeria* C, and the millerettid *Millerosaurus* B, D to show the resemblances. Redrawn from Watson. Postorbital stippled; supratemporal black; tabular cross-hatched; paroccipital process lined horizontally. F, frontal; IP, interparietal; J, jugal; L, lacrimal; J, maxilla; N, nasal; P, parietal; QJ, quadratojugal; SO, supraoccipital; SQ, squamosal.

A comparison of the millerettids, as expounded by Broom and Watson, with the captorhinomorphs, reveals a remarkable series of resemblances which are in marked contrast to the condition found in diadectomorph cotylosaurs. The skulls of captorhinomorphs and millerettids are moderately elongate and narrow, with swollen prefrontals and only moderate, occasional, broadening posteriorly; whereas those of the diadectomorphs are short antorbitally and are greatly broadened posteriorly. The dentitions of the captorhinomorphs and millerettids are unspecialized, consisting of simple conical teeth, but they have a tendency to enlarge anterior maxillary teeth to canine-like proportions. In the diadectomorphs the cheek teeth are normally greatly specialized and no caniniform teeth are known.

The manner of formation of the cheek and temporal regions is identical in captorhinomorphs and millerettids; the jugal rises high behind the orbit; the postorbital is a slender bone which passes backwards between the squamosal and parietal; the supratemporal is a slender bone which is often reduced; and the fenestration of the millerettid skulls is identical with that of the most primitive pelycosaur derivatives of the captorhinomorphs. These characters are not found in diadectomorphs with very minor and unconvincing exceptions. In these forms the postorbital remains substantial abutting against the anterior face of the squamosal (as in more primitive tetrapods) and restricting the dorsal development of the jugal; the supratemporal is either substantial or has been lost entirely (according to interpretation), and no fenestration is known, unless *Bolosaurus* is in fact a diadectomorph when the unique fenestration is quite distinct from that of millerettids and synapsids.

In nearly all respects the occiputs of typical captorhinomorphs and of millerettids are remarkably similar. The interparietals and tabulars are occipital, as are, to a slight extent, the supratemporals. With the exception of *Captorhinus* itself, the supraoccipital is broad in both groups, and the lateral extremity of the paroccipital process fails to meet the dermal bones except, perhaps, through a cap of cartilage. In two characters the quadrates of the millerettids resemble those of typical diadectomorphs rather than typical captorhinomorphs; the articular condyle lies anterior to the basioccipital condyle, and the dorsal development of the quadrate is exposed posteriorly.

So far as they are known the palates of the millerettids resemble those of the captorhinomorphs, being essentially primitive, but, in one feature, the appearance of the basisphenoid-parasphenoid complex in ventral view, they are most remarkably alike. When these structures, as described by Broom and Watson in the millerettids and by Price (1935) and Olson (1951) in captorhinomorphs are compared, the similarities of the anteriorly directed basipterygoid processes of the basisphenoids, and the elongated basal plates of the parasphenoids with, typically, a median, posteriorly directed process partly underlying the basioccipital, are seen to be almost identical. No such close similarity can be found among diadectomorphs with the possible but doubtful exceptions of the disputable form *Bolosaurus* and the procolophonids *Nycteroleter* and *Owenetta*.

When the cranial characters of the millerettids are compared with those of captorhinomorphs and diadectomorphs the resemblances to the former are numerous and striking (see Table 1) and the occasional partial likenesses to the latter, when examined in detail, are quite unconvincing. Some of the resemblances are not characters on which, by themselves, much weight would be placed by experienced taxonomists (e.g. the dentitions), but taken together the resemblances are such as to show beyond reasonable doubt that, unless good reasons to the contrary can be found elsewhere, the origin of the millerettids must be expected to lie among, or close to, the Captorhinomorpha.

The postcranial skeleton of *Millerosaurus* is essentially that of a primitive reptile of small size and slender build, and its generalized condition does little to help in deciding its relationships. Only one character is of particular interest. The single coracoid of *Millerosaurus* resembles that of the diapsid, and certain other, reptiles and contrasts with the two coracoids of captorhinomorphs. But it also contrasts

TABLE I.

	Skull moderately elongate or narrow	Prefrontal boss or swelling	Jugal high posteriorly	Postorbital slender extending posteriorly	Supra-temporal slender or greatly reduced	Synapsid fenestration	Teeth conical, pointed	Anterior maxillary teeth enlarged	Tabular & inter-parietal largely or entirely occipital	Supra-occipital broad	Para-sphenoid-basi-sphenoid complex modified
Limnoscelis	P	—	—	+	P	—	+	P	+	+	—
Protorothyris	+	+		+	+	—	+	+	+	+	
Romeria	P	+	+	P	+	—	+	+	+		
Captorhinus	P	—	+	P	+	—	+	P	+	—	+
Primitive Pelycosaurs	+	+	+	+	+	+	+	+	+	+	?
Mesenosaurus	+	—	P	+	+	+	+	+	?		
Milleretta	+	+	+	+	+	?	+	—	+	+	+
Millerettops	+	+	+	+	+	—	+	+	+		
Millerettoides	P		+		+	—	+		+		
Millerosaurus	+	+	+	+	+	+	+	?	+	+	+
Nanomilleretta	+				+			+			
Diadectes	P	—	—	—	—	—	—	—	—	+	—
Bolosaurus	—	+				—	—	—	+	P	?
Pareiasaurus	—		— E	—	—	—	—	—	—	—	—
Nanoparia	—		—	—	—	—	—	—	—	—	
Nyctiphruretus	—	—	+	—	—	—	+	—	+	—	—
Nycteroleter	—	—	+	—	—	—	+	?	?	—	?
Owenetta	—	—	—	—	—	—	+		+?		?
Procolophon	—	—	—	—	—	—	—	—	+	—	—

E = exceptions exist. P = character partially developed. ? = some evidence of character.

with the double coracoids of pareiasaur and procolophonid diadectomorphs, and the problem of the evolution of the double and single conditions in reptiles remains unsolved. The single coracoid gives no indication of the animal's origin, and, in fact, serves only to lend support to Watson's claim that the diapsids were derivatives of the millerettids.

It seems quite clear, therefore, that only the structure of the middle ear and, possibly, the position of the inner ear, can be used to support a claim to relationships between the millerettids and the diadectomorphs, and that if this fails the evidence is overwhelmingly in favour of captorhinomorph affinities.

The outstanding characters in which the middle ear region of the millerettids resembles that of diadectomorphs are the anterior position of the quadrate and the exposure of the dorsal component of the bone posteriorly. The forward movement of the quadrate is a very common modification in vertebrates. It occurs in the Dipnoi and the crossopterygians ; it is almost universal in the amphibia ; and it is found in a wide range of reptiles including the therapsids and Icthyosauria as well as the diapsids (though it is not present in the primitive form *Youngina*). Moreover Watson's (1954) restoration of the skull of the primitive captorhinid *Protorothyris* shows that it was present to some degree in that form, and it would appear plain that such a modification could occur easily in other captorhinomorphs, and in their descendants, and is not one on which much weight can be placed.

The exposure of the dorsal component of the quadrate by a separation of the squamosal from the quadrate ramus of the pterygoid is characteristic of nearly all diadectomorphs, being found in *Diadectes*, the pareiasaurs, and, apparently, the procolophonid *Nyctiphruretus*. But it has not occurred in the procolophonids *Nycteroleter* and *Procolophon* (unless the condition of the squamosal in these forms can be interpreted as secondary) and would appear likely, therefore, to have been achieved independently within this group. And the extreme specializations of *Diadectes*, with the head of the quadrate attached to the pro-otic in a unique manner, suggest that it is not closely related to other diadectomorphs, and that here too the posterior exposure of the quadrate may well have been achieved independently. Furthermore, an examination of the quadrate region of the captorhinomorphs shows that the condition is such as to have allowed the derivation of the millerettid condition quite simply.

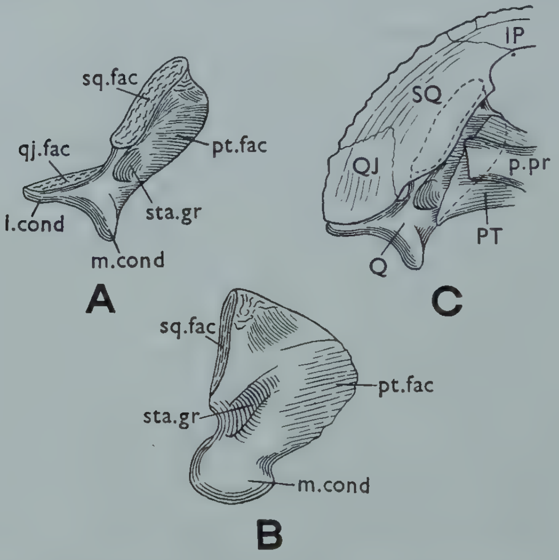


FIG. 7.—The quadrate of *Captorhinus*. A hind view, B median view, and C in position, × 2. IP, interparietal ; PT, pterygoid ; Q, quadrate ; QJ, quadratojugal ; SQ, squamosal. *l. cond.* lateral condyle ; *m.cond.* medium condyle ; *p.pr*, paroccipital process ; *pt.fac*, pterygoid facet ; *qj.fac*, quadratojugal facet ; *sta: gr*, stapedial groove ; *sq.fac*, squamosal facet.

Only in *Captorhinus* itself are the structures and relations of the quadrate known in detail, the condition in such earlier and less specialized forms as *Protorothyris* being uncertain. The quadrate of *Captorhinus* consists of a condylar region, with two poorly differentiated condyles; and a dorsally and slightly medianly directed sheet of bone which arises from above the inner condyle (fig. 7). Posteriorly the dorsal sheet of bone forms a thickened and roughened edge which was attached to the inner surface of the occipital wing of the squamosal, and anteroventrally there is an extensive facet for the attachment of the quadrate ramus of the pterygoid. This condition is not unlike that found in early amphibia, but the pterygoid has lost its attachment to the squamosal, exposing the quadrate somewhat in occipital view. The arrangement found in millerettids could be derived from this condition quite simply by a further reduction of the occipital wing of the squamosal except in the region where it supports the dorsal extremity of the quadrate, together with a shallowing of the quadrate ramus of the pterygoid. Furthermore there is a roughening of the median face of the uppermost part of the dorsal sheet which suggests that, as in the millerettids, the squamosal actually enclosed the tip of the quadrate medianly (cf. Watson 1954, fig. 15). It appears plain that the condition of the quadrate and its manner of attachment in captorhinomorphs cannot be considered to debar these forms from possible ancestry of the millerettids.

The millerettid stapes is now well known, having been described by Watson very fully in *Millerosaurus nuffieldi*. Here it is a stout bone, perforated for the stapedial artery, and having three distal processes. There is a dorsal process for attachment to the paroccipital process, an anteriorly directed processus internus for attachment to the quadrate, and a process which is directed outwardly and slightly ventrally. Watson interpreted this latter process is one for the attachment of the hyoid, and supposed that a cartilaginous extrastapes as present on the roughened distal end of the stapes, but since the hyoid attachment is usually lost in adult reptiles, it would appear simpler to interpret the ossified process as the extrastapes and the roughened area as indicating the hyoidean attachment.

The stout form of the stapes results partly from the small size of the animal which causes the brain case to bulk large in proportion to the size of the skull and so cause the middle ear region to lie close to the quadrate (Watson, 1931). All three stapedial processes are recognizable, each having been recorded in *Captorhinus* itself if the laterally directed process may be equated with the boss on the distal end of the bone of that animal (Parrington, 1946). Moreover, whether Watson's hyoidean process or his hypothetical cartilaginous tympanic process be accepted as the extrastapes, the attachment of the stapes to the tympanum was behind the lower half of the quadrate, a ventral position which is in accordance with the presumed low, postquadrate position of the tympanum in captorhinomorphs, but denies any suggestion that in the " Sauropsida " the attachment of the stapes to the tympanum was in a high position (Watson, 1954).

There remains only the question of the position of the middle ear for, as Watson pointed out, in synapsids in general the fenestra ovalis lies largely or entirely below the level of the base of the brain, while in other reptiles it lies at the side of the brain case. Unfortunately little evidence is yet available concerning the level of the inner ear itself and no explanation of the position of the fenestra ovalis has yet been advanced. But it would seem possible that the position of the fenestra ovalis in captorhinids and synapsids is concerned with the dropping of the quadrate to a level far below that of the basioccipital condyle, for this modification has taken place in the primitive captorhinid *Protorothyris*, and is commonly present among pelycosaurs, and as a result the ventrally directed fenestra ovalis faces the lower part of the quadrate, so allowing the stapes to consist of a more or less straight rod leading directly to the position in which a tympanum can be assumed to have existed. This interpretation would imply that the relatively high position of the fenestra in millerettids and diapsids may be secondary.

It is concluded that the structures concerned with the ear in captorhinomorph reptiles are, so far as they are known, well suited to give rise to those recorded in the millerettids and, therefore, that the numerous and often close similarities elsewhere portray true relationships between the two groups. And, because Watson has shown that the millerettids resemble the earliest diapsid reptiles in many characters, and are well suited to be their ancestors, it must be concluded that the diapsid reptiles, like the synapsid reptiles, were derived from the captorhinomorph cotylosaurs. Neither the structure of the foot nor the circulatory systems deny this conclusion. Schaeffer (1941) has studied the morphological and functional evolution of the tarsus of reptiles and concluded that " The captorhinomorph tarsus is without question at least the structural ancestor of the eosuchian tarsus." And von Hofsten's criticisms of Goodrich's account of the reptile circulatory system support rather than deny his conclusion that the primitive amniotes, including the captorhinomorphs, must be presumed to have had a symmetrical arterial system, proper to an amphibian, and so capable of giving rise to those found in modern reptiles, birds and mammals.

But this conclusion does nothing to solve the problems of the origins of the Chelonia, the Sauropterygia and the Ichthyosauria. As Gregory (1946) has shown, the pareiasaurs have so much in common with the Chelonia that they may well represent the cotylosaur ancestors required by Watson's (1914) interpretation of *Eunotosaurus*. Nevertheless only the discovery of one or more forms clearly intermediate between the two groups will allow confidence to be placed in this, or any other, view. And in the case of the aquatic orders, great structural gaps are found when any attempt is made to show alliances, and neither order shows clear indications of relationships to either the synapsids or the diapsids. Judged from the evidence available to-day, therefore, the dichotomy of the amniotes amounts to no more than the development from primitive, captorhinomorph stock of two dominant lines of reptiles, the Synapsida and the Diapsida, leading to the mammals and birds respectively.

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THE VERSATILITY OF HEREDITY

By G. Pontecorvo, F.R.S.

(*Professor of Genetics in the University of Glasgow.*)

Introduction.

According to the Oxford dictionary, heredity is the tendency of like to beget like. It is, of course, one of the most general features of living things. At the time of the Darwin-Wallace paper there was practically no knowledge of the processes underlying it.

In respect of one of these processes—chromosomal heredity in sexual reproduction—this knowledge has become very substantial in the first 30 years of the present century. In fact, it has become so precise that it permits the use of deductive-inductive approaches to a much greater extent than in any other field of biology.

However, heredity in sexual reproduction is only one kind of heredity; an important one, to be sure, but not *the* most important. Heredity is in operation every time that a cell divides and produces two of its own kind, and, more generally, every time that a biological system is replicated.

The biological system which is replicated—and therefore shows " heredity " at work—need not be multicellular or even unicellular: there are subcellular systems (e.g. chromosomes, viruses) which show heredity. Clearly, it is necessary to introduce here some definitions before proceeding.

A biological system—be it multicellular, unicellular or subcellular—is defined as self-replicating when it plays an indispensable and specific part in its own replication; in other words, it cannot be made except from a pre-existing one, or, to use contemporary jargon, it carries essential " information " for its own replication.

A property of self-replicating systems, found in every case in which it has been looked for, is the following. The system is capable of abrupt changes, usually in many different ways, such that the changed systems are self-replicating in the changed forms. Changes which lead to a self-replicating *changed* system are called " mutations ".

In plain language self-replication is called heredity.

Recombination.

Certain processes of heredity—outstanding among them that of heredity in sexual reproduction—have a consequence of enormous biological interest: genetic recombination. That is, they lead to the combination and reassortment in one self-replicating system of information derived from two or more distinct others.

Up to about 1945—apart from *Pneumococcus* transformation (see below)—sexual reproduction was the only process known to lead to genetic recombination. But perhaps this is too rigid a statement. Stretching the definition of genetic recombination a little, certain types of virus infection, transmissible through the gametes in higher organisms, or perpetuated in a cell lineage, could qualify as processes of genetic recombination.

Since 1945 it has become firmly established that sexual reproduction is not the only process leading to genetic recombination. This has been the most salutary contribution to biological thought of the development of microbial genetics. The object of the present paper is precisely to discuss this discovery and its implications.

The novel systems of recombination discovered, or clarified, in the last 12 years are all in micro-organisms and they number at least five:

(1) recombination in viruses (foremost bacteriophage);
(2) transformation in *Pneumococcus*, *Hemophilus* and *Escherichia coli*;
(3) conjugation in *Escherichia coli*;
(4) transduction in *Salmonella* and *E. coli*;
(5) the parasexual cycle in fungi.

Genetic Information.

Before describing and classifying these novel systems, we have to consider of what a system of recombination consists.

First, there is the code, or blue-print, carrying the information for self-reproduction. Where we know something about this code—i.e. in chromosomes, viruses and transforming principles—it seems to consist of a non-repetitive (" aperiodic ") linear structure in which the items of information are singularities arising from particular sequences, arrangements or configurations along the structure.

Whether the singularities are surface configurations at supra-molecular levels, as Schmitt and Kacser suggest, or particular sequences of nucleotides of four kinds in a polynucleotide chain, as Watson & Crick suggest, is not essential for our discussion.

What is essential is what has emerged in the last seven years from genetic analysis of the fine structure of phage particles and of minute chromosome regions. That is, the discreteness of the singularities—the genes of classical genetics—need not be, and probably is not, structural ; it is a functional discreteness.

For instance, consider a hypothetical model of a continuous sequence of nucleotides with the succession of nucleotide triplets (each triplet specific for a particular aminoacid) determining the sequence of aminoacid residues in a polypeptide chain. About 1000 such nucleotides would determine the sequence of some 300 aminoacid residues in a protein, and the following 1000 in another protein. The two singularities (each determining one protein) need not result from any discontinuity in the polynucleotide chain. An actual separation between the two parts of the sequence, each specific for one protein, may not even be necessary. But if it were necessary, it could easily be achieved by interposing a " nonsense " sequence of a few nucleotides, i.e. a sequence incapable of specifying any aminoacid.

All this is, of course, speculation of a very thought-provoking type, for which we are mainly indebted to Watson, Crick and their colleagues.

The exciting fact is that we have plenty of evidence of a linear sequence of singularities—the genes—in the code : the whole of classic genetics speaks for it. To this we can now add that there is no evidence of a different kind of linear bond between the elements of one gene and those of two genes. Recombination analysis of the last seven years suggests a qualitatively continuous genetic structure for metazoa (*Drosophila*), lower plants (*Aspergillus*), bacteria (*Salmonella, E. coli*) and bacteriophage.

Differences in the code, still compatible with the self-replication of the systems are those which we recognize in heredity.

Transmission of Genetic Information.

We can now consider how the code is transmitted. We need not consider ordinary cell division in which the code is duplicated and each daughter cell inherits one copy. We shall consider only cases in which the code, or part of it, is transmitted from or exchanged between, one cell lineage and another one.

In sexual reproduction this is achieved by fertilization, i.e. a complete code (essentially a haploid chromosome set, or " genome ") from one cell lineage combines with a complete code from another cell lineage. In species with an extended diploid phase, the two codes are replicated side by side for innumerable cell generations without exchanging items of information in which they may differ, except as the consequence of rather rare events of mitotic recombination and segregation (see further on).

In sexual reproduction the reassortment of the two codes is achieved at meiosis. From the two codes four complete ones arise but each is made up of a reassortment of homologous parts of those two, which are replicated in the process.

A regular alternation of fertilization, or better karyogamy, and meiosis defines sexual reproduction. When it goes with an extended diploid stage, sexual reproduction achieves two vital functions : storage of variation and recombination.

Storage of variation is the consequence of " dominance ", i.e. if the two codes in one cell lineage differ in one (or more) items of information, so that there are two alternative messages, the cell responds to only one of them, referred to as " dominant ". This is a way of saying that in respect of a large number of items diploid cell lineages may be differently heterozygous and yet show no corresponding differences in phenotypes.

Recombination is the consequence of certain features of meiosis, i.e. crossing-over and random reassortment of non-homologous chromosomes. Fertilization, storage of variation in heterozygotes and recombination together make it possible for individuals of an interbreeding group to share a common heritage, to draw from a common pool of genetic information.

We shall consider now in which ways the novel systems of genetic recombination discovered in recent years differ from sexual reproduction in any one or more of three respects. First, in the way genetic information is transmitted fom one lineage to another one ; second, in the way in which the genetic information received is incorporated and stored with that of the recipient, and third, in the way in which the genetic informations of donor and recipient are recombined.

As to the transmission of the genetic information, the most striking feature of most of the novel systems of recombination is the following. In sexual reproduction a complete code (" genome ") passes from one cell lineage to another one ; in four out of five of the novel systems only *parts* of the code go over in each act of transmission. These parts may range from rather small portions of the total genome, e.g. in phage mediated transduction, to almost all of it in a small proportion of the acts of conjugation in *Escherichia coli*.

The very acceptable term " merozygote " has been suggested by Wollman, Jacob & Hayes for the entity resulting from transmission of only part of the code. The product of complete transmission—as in sexual reproduction and in the " parasexual cycle " in fungi (see below)—can be called " holozygote ".

Merozygotic processes of transmission are the " transformations " in *Pneumococcus* and *Hemophilus* in which only a fragment of the desoxyribonucleic acid of a donor cell enters a recipient cell. How big, or small, this fragment is, is not yet known. The recent development by Chargaff and his colleagues of a technique for transformation in *Escherichia coli* should soon permit this to be found out. *Escherichia coli* is the only bacterium in which extensive genetic maps based on conjugation (see below) are available. It will be interesting to know how big a fraction of the map can be covered by a single transforming fragment.

Another merozygotic process is that based on conjugation in *Escherichia coli*. Its discovery by Lederberg & Tatum in 1946 is probably the most outstanding feat so far in microbial genetics. It was at first supposed to consist, like fertilization in higher organisms, of the fusion of two cells. The brilliant work of Wollman & Jacob has shown that it is, instead, of the nature of a polarized entry into a recipient cell of part or all of the (single) chromosome of a donor cell.

This entry can be interrupted, either artificially by mechanical agitation or naturally by unknown events, at any time after its inception. Hence, the resulting merozygote carries a portion of the donor's chromosome which is of length proportional to the length of time for which conjugation lasted. Because of the polarized entry of this chromosome, the genes along it enter the recipient cell in a queue and their positions can be deduced from their time of entry. This novel way of " mapping " chromosomes has permitted Jacob & Wollman to go further. They have measured the number of phosphorus atoms between one gene and another one by using a ^{32}P-labelled donor chromosome.

A third merozygotic process is that of bacteriophage-mediated transduction in *Salmonella* and *Escherichia coli*, discovered by Zinder & Lederberg. In this process the genome of a cell is fragmented as a consequence of lysis due to the maturation of the bacteriophage. A bacteriophage particle can carry any one of these fragments into a recipient cell. If the bacteriophage enters into symbiotic relations (" lysogeny ") with the recipient cell, the fragment of bacterial genome it carried may be incorporated by the recipient cell and replicated.

The use of this technique has permitted Demerec and his group, and Morse and the Lederbergs, to carry out genetic analysis to an extraordinary degree of refinement in *Salmonella* and *Escherichia coli*, respectively.

In the genetic processes of recombination in viruses, and particularly in bacteriophages, the nature of the stage comparable to a zygote is not known. However, the work of Hershey & Chase and that of Levinthal suggests that only part of *both* parental genomes is present in the particles from which recombinants originate. If this interpretation is correct, the system of zygote formation in bacteriophage would be classified as merozygotic.

Among the novel systems of recombinations the only one which is not merozygotic is the parasexual cycle discovered by Pontecorvo & Roper in fungi. Here haploid nuclei pool their whole genomes to give a diploid " holozygote ": the origin of the holozygote differs only in non-essential details from that of a holozygote produced in an ordinary sexual cycle. The real difference between the parasexual cycle and the sexual cycle does not lie in the mode of formation of the zygote. As will be seen, it lies in the way the information from the two nuclei that fused is recombined and sorted out again.

Storage and Sheltering of Genetic Information.

This is an aspect of the novel systems of recombination which is still very poorly understood. We have no idea, for instance, of what processes operate in this respect in viruses and bacteria.

In the parasexual cyle in filamentous fungi this knowledge is beginning to take shape. We know, for instance, that genetic information can be stored in two ways. One is the same as in sexual reproduction in higher organisms with an extended diploid stage, i.e. heterozygosis. The other, which does not occur in higher organisms, is heterokaryosis, i.e. the coexistence in multinucleate cells of nuclei of more than one genotype.

An old preconceived idea was that asexual filamentous fungi did very well with an exclusively vegetative haploid life-cycle, with no provision for recombination and for storing and sheltering of gene variation. It was supposed that because of their short generation time, and of their haploid nuclei exposed to immediate selection, mutation alone in a clonal system of reproduction was all that they needed for evolutionary adaptation.

The real situation has turned out to be quite different. The few asexual filamentous fungi which have been investigated have, just as higher organisms, devices for the storage and sheltering of gene variation and for recombination. In fact, in respect of storage and sheltering of variation they are better off than higher organisms : they have two ways of doing it instead of only one.

As to the other novel systems, one point is worth keeping in mind, i.e. that in colonial organisms a good deal of intercellular complementarity operates. The most obvious example of it is syntrophism between cells with different nutritional requirements. But the microbiological literature is full of examples of all kinds of interactions between cells, some very subtle, which permit the survival for many cell generations of cells which, by themselves, would be ruthlessly eliminated.

In bacteria and viruses systems of sheltering of gene variation based on something like diploid heterozygosis or haploid heterokaryosis may well play only a small role. On the other hand, the scope of intercellular or inter-particle interactions is probably quite large, and it may be profitable to probe in this direction.

Recombining and Sorting out of Genetic Information.

Once the information of one cell lineage has been transmitted to another one via a merozygotic or a holozygotic process, the two informations can be carried on in duplex condition for a definite or indefinite, large or small number of replications. Ultimately, however, the simplex condition must be restored in order that the whole process may be repeatable.

This process of reduction from duplex to simplex is, of course, one of the result of meiosis in organisms with a standard sexual cycle.

But there is more. In meiosis reduction *inescapably* entails *one kind* of recombination between corresponding parts of the information from each parental code : i.e. recombination between members of non-homologous chromosome pairs. It also entails *usually* recombination between fractions of the parental codes smaller than whole chromosomes, i.e. recombination of non-homologous segments of homologous chromosomes : this intra-chromosome recombination is the result of crossing-over.

Thus in meiosis reduction and recombination are co-ordinated, in fact they are parts of one process.

This is by no means so in at least one of the novel systems of recombination, the parasexual cycle in fungi. In this system, reduction to the simplex condition ("haploidization") and recombination of whole non-homologous chromosomes are, as in meiosis, the twin results of one and the same process. But intra-chromosome recombination—the consequence of mitotic crossing-over—is not co-ordinated at all with that process. What happens is that in a small proportion of diploid nuclei in a clone haploidization takes place ; in another small proportion mitotic crossing-over takes place. The coincidence of both in one nucleus or in one cell lineage is no more than accidental.

In the other four novel systems of recombination—recombination in viruses, and transformation, transduction and conjugation in bacteria—it looks as if the genetic information were based on a single linear code : by analogy, a single "chromosome". However, because of the techniques used for the analysis of recombination in these systems, it is not yet clear whether or not reduction and (intra-chromosomal) recombination are inescapably linked as in meiosis, or independent events as in the parasexual cycle in fungi.

Classification of the Systems of Recombination.

The rudimentary knowledge available on the details of the novel systems of recombination makes generalization hazardous. Nevertheless, the discussion in the preceding sections permits an attempt to classify the kinds of system which are conceivable.

Clearly, there are two aspects of a system of recombination which have to be considered : one concerns the mode of formation of the zygote, which can be, as we have seen, merozygotic or holozygotic ; the other concerns the modes of reduction and recombination (intra-chromosome) which can be co-ordinated or not.

We have, therefore, a two-by-two series of relations :

		Mode of formation of the "zygote"	
		Holozygotic	Merozygotic
Mode of recombination and reduction	Co-ordinated	1	2
	Unco-ordinated	3	4

Sexual reproduction as it occurs in higher organisms, in certain fungi, unicellular Algae, Protozoa etc., falls into Class 1 : holozygotic, with reduction and intra-chromosome recombination co-ordinated (meiosis). The parasexual cycle in fungi falls into class 3 : holozygotic, with reduction and recombination unco-ordinated (haploidization and mitotic crossing-over).

Transduction and transformation in bacteria, are merozygotic. In fact, Lederberg originally coined the term transduction for the transmission of a genetic fragment, i.e. what we now call a merozygotic process. This definition included, of course, transformation as in *Pneumococcus* and, now that more is known about it, it would include conjugation in *Escherichia coli*. The term transduction, however, has been generally used in a more restricted sense : virus-mediated transmission of a genetic fragment. Whether transduction and transformation belong to class 2 or to class 4 cannot yet be decided.

The system which involves conjugation in *Escherichia coli* is usually merozygotic, but in a proportion of cases it may be holozygotic : i.e. when the whole chromosome of the donor succeeds in being incorporated. Again, it cannot yet be stated whether in this system reduction and recombination are co-ordinated or not.

In bacteriophage "mating" is probably merozygotic and recombination is probably co-ordinated with reduction. The phage system, thus, would fall into class 2.

Conclusions.

Many basic biological questions arise from the discovery of the five novel systems of recombination enumerated here. One will be singled out for speculation. Do any of those systems, in whole or part, occur regularly or as an exception in higher forms?

The answer is already available in respect of the parasexual cycle in fungi. This occurs side by side with the sexual cycle in some species of fungi, and replaces the latter in others. One of the processes on which it is based—mitotic crossing-over—occurs in a metazoon, *Drosophila*, in which it was discovered and analysed by Stern 20 years ago.

Reports of the occurrence of crossing-over and segregation in somatic cells of higher organisms including man have appeared sporadically in the literature. Of course, somatic mosaic patches of recessive phenotype can occur in diploid heterozygotes as a consequence of a number of processes. Somatic crossing-over is only one of them : mutation, abnormal distribution of chromosomes, etc., can all produce the same phenotypic effects. It is, however, a fact that mosaic patches are rare in higher organisms. They would be most inconvenient and natural selection has seen to it that they do not occur abundantly.

In the evolution of the extended diploid condition segregation in somatic cells must have been strictly controlled. A corollary to this, as I suggested some years ago,is that in organisms not used to be diploid, i.e. without an extended diploid stage, somatic segregation should occur readily if given the chance. This is precisely what happens in fungi when we make diploid their (usually haploid) vegetative nuclei.

We can go further and conceive of exchanges (be they by a process of breakage and reunion or by one of copying-choice) as a *necessary* concomitant of the replication of the genetic code. We can also conceive that replication requires the pairing of two homologous structures, as Stent has suggested with a detailed model.

This requirement for pairing would raise difficulties with haploid organisms unless the elementary code were itself a double structure. Electron microscopy seems to lend support to this possibility. Ris showed that in deproteinized chromosomes the smallest unit discernible is a fibre about 40 Å thick made up of two fibrils : the juxtaposition of two homologous structures seems to be there ready made.

The next step in these speculations is to assume that the pairing, necessary for the replication of one elementary fibre and provided by its two fibrils, may be provided occasionally in diploid organisms by pairing between fibrils of two homologous fibres.

These speculations view the elementary process underlying exchanges as very primitive, perhaps as primitive as self-replication of a linear genetic code. In the course of evolution this process has come to be used for recombination in heredity. But recombination had to be suppressed in the soma as evolution of an extended diploid stage progressed. The only cells in which it had not to be suppressed were the gonia. It should not be impossible, thus, to provide experimental conditions which remove what blocks recombination in somatic cells.

In conclusion, the study of recombination in somatic cells is likely to throw some light on the evolution of heredity. It is also likely to provide by-passes to the long generation time of slow-breeding organisms like man.

In lower organisms formal genetic analysis and map construction has already been performed by Pontecorvo & Käfer by using mitotic, instead of meiotic, recombination. If there is any basis for the above speculations, the way is open to formal genetic analysis in man based on mitotic recombination in tissue cultures.

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FOSSIL PLANTS AND EVOLUTION

By H. HAMSHAW THOMAS, F.R.S.

Introduction.

The geological record of plant life on the earth as known to Darwin and Wallace provided no support to the theory of Evolution. It showed plant remains in the Tertiary and Upper Cretaceous rocks which could be closely matched with living genera of flowering plants and conifers: the fossil vegetation of the Mesozoic period appeared to consist only of ferns, cycads and conifers; while in the Carboniferous period the earth was thought to have been clothed with plants referable to the vascular cryptogams. Very little was known of the structure and reproduction of any fossil forms, most of which were referred to living groups on some similarity of external appearance.

The publication of the *Origin of Species*, and the discovery in certain coal seams of well-preserved petrified plant remains, gave a great impetus to palaeobotany in Britain and its study was taken up by several eminent botanists led by W. C. Williamson. The work of D. H. Scott, R. Kidston, A. C. Seward and F. W. Oliver provided a mass of information which was much more reliable than that previously available. At the opening of this century Oliver and Scott showed that many of the fossils previously regarded as the remains of ferns were in fact gymnosperms with complex ovules and tassels of pollen-bearing sporangia.

In 1909 D. H. Scott, then President of the Linnean Society, surveyed the bearing of contemporary knowledge on the doctrine of Evolution. He expressed the view that the records of plant history suggested a connection between some of the main groups of living forms, but that they provided little evidence of the derivation of one species or genus from another. Since then our knowledge of the plants of past ages has increased enormously, both by the discovery of forms not previously known and by the investigation of the structure and reproduction of types only known previously from leaf impressions. A successful search for plant remains in the Upper Silurian and Devonian rocks produced examples of great evolutionary significance. The discovery of petrified remains in the Coal Measures of North America has enriched our knowledge by some 150 species (Andrews, 1951). Large collections have been made of Mesozoic plants in various parts of the world, which have given a new view of the vegetation of this period, and the study of Tertiary and Quaternary remains have shown the changes which took place in plant life at a comparatively recent date.

Research has been greatly assisted by the introduction of new technical methods for the microscopical examination of fossil plants. Nathorst and his pupils improved the old method of macerating carbonized remains, and showed their great value in the study of Mesozoic plants. The discovery and perfection by Prof. Walton of a way of preparing thin sections of petrified material by the peel method gave considerable impetus to the study of such remains. It placed the production of series of thin sections within the easy reach of almost any worker.

We know so much more about the plants of the past than our predecessors that it may be useful to consider the bearing of our present knowledge on the theory of evolution.

Changes in the World's Vegetation.

An important argument for the theory of evolution was based on the evidence from the geological record which showed that many species formerly living in the world had become extinct while other new species, genera or classes had made their appearance. It was held by some that the plant record did not show this with any certainty. Many genera of flowering plants can be traced back to the Upper Cretaceous, while the living species of *Ginkgo*, *Taxus* and *Marattia* are very similar to forms of these genera found in Mesozoic rocks. But there can now be no doubt that since Devonian times there have been a series of complete changes in the plant covering of the earth.

Darwin (1888) thought that " the geological record, at all times imperfect, does not extend far enough back to show with unmistakable clearness that within the known history of the world organisation has largely advanced ". Fifty years ago Scott (1909) considered that this statement was still true. But the discovery of fossil plants in the Silurian and Lower Devonian rocks has greatly changed the outlook. In these forms we have unmistakable evidence of the existence of plants with little external differentiation and with a simple anatomical structure ; there were no fully differentiated leaves, and the simple sporangia terminated the main axes or side branches. It has been suggested that the simplicity of some of these forms was due to reduction, but in view of the number of different genera now known, this is unlikely.

After Kidston & Lang published in 1917 their remarkable description of the Rhynie plants it seemed that the Psilophytales might well be the ancestors of all the higher plants, especially when this was followed by further discoveries of somewhat similar simple types. But these forms are probably not members of a single group of closely related types ; they should be regarded (Leclercq, 1954) as representatives of several phyletic lines from which later groups of the Pteridophyta developed. Although showing differences in form and anatomical structure all these types display an unmistakably primitive organization which suggests their origin from algal ancestors.

It is worth noting that these early land plants are accompanied by the remains of thallophytic forms, which exhibit considerable size and complexity but show no trace of the differentiation of xylem, the characteristic feature of land plants. The long known trunks composed of tubular elements and called by the inappropriate name of *Prototaxites* have now been found in several parts of the world and in some places appear to have flabellate branches. They have been referred to the Phaeophyceae, but on inadequate grounds. Another interesting type is Lang's *Nematothallus* (Lang, 1937) which had a flat frond-like expanse of tissue composed of interlacing tubes, often of two distinct orders of size, and covered by a cuticle with a pseudocellular pattern. Within the cuticle and among the tubes were firm walled (cuticularized) spores of various sizes. Another curious form, described by Andrews & Alt (1956) as *Crocalophyton*, had a unique structure with radially elongated strands. This also shows that thallophytic forms had developed considerable size and complexity by Silurian times. We now know that plants resembling Algae had long been in existence for Tyler & Barghoorn (1954) have described indubitable remains of filamentous plants from the Pre-Cambrian of Southern Ontario which are perhaps 1300 million years old. These and the varied remains of thallophytic plants from the Cambrian rocks show that the pteridophytic plants may well have evolved from thallophytic forms long before their appearance in Silurian times.

Interrelationships of the Pteridophyta.

The general similarities in life-history and in the reproductive structures of the different groups of the Pteridophyta provided grounds for considering that the Ferns, Lycopods, Equisetums, Sphenophylls and *Psilotum* were probably derived from a common ancestor. In the early part of this century much thought and discussion was devoted to this matter. It was rendered more complicated by the morphological dogma that all sporangia were borne on sporophylls of a more or less leaflike nature.' Our present evidence shows however that these groups have been quite distinct from Devonian times and that each has evolved independently. The Lycopods have shown relatively little change in their sporophytes, apart from variations in size and minor changes in anatomical structure. The ferns, on the other hand, have developed in a great number of ways, in form, size, anatomical structure and sporangia. The Equisetales and Sphenophyllales are perhaps interrelated, both having verticillate construction and similarities in their fertile shoots and sporangia, but they were already distinct in Devonian times. The discovery of early examples of the fertile shoots of these forms, in which the sporangia were borne at the tips of naked branches and not on leafy sporophylls, indicates the futility of the older discussions about the morphological nature of their Carboniferous cones. It was almost impossible to interpret the many known forms of these structures on the sporophyll theory. The historical record now seems to show that their bracts were not sporophylls but arose on the fertile axes between the sporangiophores. Mesozoic and modern members of the Equisetales lack any such bracts and retain the primitive structure.

The members of the Pteridophyta have shown some parallel evolution in the development of their spores. Each group has at some time developed heterospory, though most of the forms with this character have become extinct.

Origin of the Seed-bearing Plants.

Before the coming of evolutionary ideas taxonomists regarded the possession of seeds as an indication of affinity, and this view persisted well into the present century, when affinity had come to mean genetic relationship. Now, however, the view is widely held that the seed habit originated independently in different groups of plants. D. H. Scott pointed out that the integumented megasporangia which were formed in at least two genera of Palaeozoic Lycopods, were seeds in a biological sense. From the same period we find remains of two other great groups of plants which produced seeds, these were the Cordaitales and the Pteridospermae. They were totally different from one another in general form, in anatomical structure, and in the the arrangement of their fertile structures, they cannot be considered as closely related. Both had ovules of a primitive type, but in the Cordaitales the integument was derived from a pair of opposite members (bracts or branches), while the pteridosperm integument was formed from the members of a whorl, five or six in number. These structures grew just below the megasporangium on the fertile axis, and in some forms were concentric in anatomical structure and free from each other at their tips. I consider that we should not regard these structures as modifications of some pre-existing organs but new formations on the fertile apex. It seems likely that the later pteridosperms, the Bennettitales, the Cycads, and probably the angiosperms, were derived from plants having seeds of this type, while the Coniferales, Taxales and perhaps the Ginkgoales, sprang from plants with the Cordaitean type of seed.

Emberger (1949) has drawn attention to the absence of any embryos in the petrified ovular structures from the Upper Palaeozoic rocks. He therefore considers that, contrary to past usage, they should not be described as seeds ; he proposes a new class, the Prephanerogams, for the plants having these ovules and includes in it the Ginkgoales and Cycadales. It may well be that from an evolutionary point of view a useful distinction may be drawn between plants in which the embryo is only developed after the dispersal of the ovule (seed), and those in which full development occurs in attachment to the fertile branch. But differences of this kind cannot be held to indicate a genetic connection between such diverse groups as the Cordaitales and pteridosperms, or a separation of the Bennettitales from Cycads and pteridosperms. It may be that none of the earlier seed plants, including the conifers, completed the formation of embryos on the parent plant, but it is unlikely that we yet know all the facts relating to this problem.

Mesozoic Gymnosperms.

The discovery during the last half century of six or more types of plant which flourished in Mesozoic times and bore seeds (ovules) has been one of the most important of the recent contributions of palaeobotany to our knowledge of plant evolution. Formerly only the conifers, ginkgos, and Bennettitales were known from this period. The existence of the Cycads was inferred from the remains of leaves, many of which have since been shown to belong to the Bennettitales, but their reproductive structures were virtually unknown. The work on the Mesozoic gymnosperms has given quite a new conception of the evolutionary changes which seem to have taken place among many of the megaphyllous seed plants about the end of the Palaeozoic period. Some of these changes may be significant when the origin of the angiosperms is being considered.

The well-known work of Prof. Florin (1938–45) has greatly elucidated the history of the Coniferales which were widespread at this time, with Araucarian elements especially abundant. Various genera of the Ginkgoales were plentiful during Triassic and Jurassic times, as shown by their characteristic leaves, but we have as yet little certain knowledge of their reproductive structures. Prof. Harris (1951) has furnished good evidence for thinking that the simple or forking linear leaves known as *Solenites* or *Czekanowskia*, and previously thought to be allied to the Ginkgoales, had fructifications of a unique type which he referred to the genus *Leptostrobus*. They show a slender axis bearing fertile appendages in a loose spiral ; each fertile structure formed a flattened capsule composed of two valves joined at their base and containing about five seeds. The micropyles of the seeds faced the axis, and pollen was also found within the valves.

The problem of the evolution of the Cycadales has been little advanced by the discovery of the male and female cones of these plants. Both were very similar to those of living types, though in *Beania* the seed-bearing structures did not form a compact cone.

The Bennettitales have proved to be more varied in form and structure than had been suspected. The earlier types had elongated stems with widely separated leaf bases, unlike those of the Lower Cretaceous Cycadeoideas. The leaves were pinnate or entire. The " flowers " were terminal structures, sometimes on a naked peduncle they frequently had a spiral group of bracts just below the fertile organs. Some of the flowers were unisexual, others bisexual. The male sporangiophores show considerable variation in form but the ovulate parts are remarkably uniform. Some evidence suggests that the characteristic interseminal scales originated from sterile ovules, nothing has been found to suggest that they ever had the nature of bracts or sporophylls.

One of the new groups is the Pentoxylae, an assemblage of plant remains from the Jurassic rocks of India preserved in a petrified condition. Our knowledge of these peculiar types is due to Sahni (1949) and his pupils (Vishnu Mittre, 1953). The stems had an unusual structure with five or more steles and closely-packed leaves, which were probably entire elliptical structures reaching a length of 7 cm. The female infructescences were branched and had compact cone-like structures at the ends of the branches ; each cone consisted of a number of closely-packed seeds with thick integuments and the remains of micropyles projecting to the outside. The pollen was produced in rounded sporangia terminating the branches of slender elongated structures, which arose from the apex of a stem and may have been fused at their bases. These plants seem morphologically distinct from any other known type, though a comparison with the Bennettitales is suggested.

Another new group from the Triassic of the Southern Hemisphere has been named the Corystospermaceae (Thomas, 1933). These plants were essentially similar to the Palaeozoic pteridosperms. Their leaves varied considerably in form, from bipinnate to simple, and they had separate male and female inflorescences. The latter were branched, the branches being either in one plane or spirally arranged. The female structures bore bracts and bracteoles, their branches terminated in recurved cupulate ovules with projecting micropyles. The branches of the male inflorescences were expanded at their tips and produced a number of elongated sporangia on their lower surfaces. The pollen grains were winged, probably an adaptation for the fertilization of the pendulous ovules by a drop mechanism. When ripe the seeds had a stout testa.

The Peltaspermaceae have been found in both the Northern and Southern Hemispheres; they had well-cutinized bipinnate leaves, known as *Lepidopteris* (Harris, 1932). Their pollen was borne in short sporangia formed at the tips of a branched structure and sometimes showing a radial arrangement. The ovules were produced on peltate structures at the ends of branches which arose spirally from a central axis.

The Caytoniales (Thomas, 1925; Harris, 1940) were a somewhat later group in the Northern Hemisphere. Their leaves were compound, having four or fewer leaflets with closed reticulate venation. The male and female inflorescences were branched in one plane and fertilization was gymnospermous. The pollen was produced in elongate loculate sporangia like the anthers of some flowering plants. The ovulate branches ended in small cupular structures containing a number of ovules and having a small opening at their base near the stalk. After fertilization this opening became completely closed and the structure developed into a fleshy berry-like fruit containing many seeds with stony testas. This group is interesting because it shows several structural and biological features seen in the angiosperms. The present writer has been widely credited with the view that the Caytoniales may be the ancestors of the flowering plants, in spite of his clear statement on the subject (Thomas, 1931). He considers the Caytoniales to be descended from the Pteridosperms, like the Cycadales and Bennettitales; the angiosperms probably arose independently from the Palaeozoic pteridosperms, and the features that they show in common with the Caytoniales are due to parallel development.

A quite different and highly problematical form, which may well have been a seed plant, was abundant in Permian and Triassic times in the Southern Hemisphere and India. Its leaves have long been known as *Glossopteris*, but this is a form genus, and two or more types of plant had leaves of this character. The reproductive organs of several species have been described by Mrs. Plumstead (1956) from impressions in which almost all the remains of plant tissue have disappeared. In these specimens a short fertile axis sprang from the midrib of the leaf and terminated in a close conical group of contiguous seed-like bodies enclosed in a bivalved envelope. Mrs. Plumstead thinks that the seed-like structures grew on the valve nearest to the lamina and that the other valve gave rise to large pollen-bearing structures. The specimens seem to justify this interpretation, but as no other plant is known to have a similar morphological construction the discovery of examples showing remains of the plant tissue is most desirable. In any event it seems likely that the material with the Scutum or Ottokaria type of reproductive organ, represents another distinct type of seed-bearing plant, previously unknown.

Other, more scanty, remains have been found in South Africa and elsewhere which show that seed plants had appeared in considerable variety by the end of the Triassic period. It is not improbable that the *real* ancestors of the angiosperms may yet be found to have occurred at the same period, for many hundreds of square miles of plant-bearing strata in southern Africa still remain to be examined.

The Problems of Plant Phylogeny.

If phylogeny is defined as the racial history of a species or genus, the historical record of plant life provides almost no evidence for its study. This is because we are very seldom able to give a complete description of a fossil species. Our material consists mainly of isolated organs, separate from one another, and we can rarely be sure of linking up the stems, leaves and reproductive structures to show what the complete organism was like. If a species cannot be defined in the same way as a living plant, the form of its ancestors or progeny is always a speculation.

In this situation two different methods have been followed by those interested in phylogenetic studies. Both of these aspects have been fully discussed by Zimmermann, whose writings have been largely responsible for the interest shown by an increasing number of botanists in the bearing of palaeobotanical knowledge on our understanding of plant evolution. One mode of phylogenetic study is the examination of the probable relationships of the major groups of land plants, a second is concerned with the historical study of the forms and characters of organs of the same kind in one or a few closely related taxonomic groups.

The problems of the interrelationships of the larger groups of extinct and recent plants have given rise to a considerable literature. Phylogenetic schemes have been put forward by Zimmermann (1930), Lam (1955), Emberger (1944), Magdefrau (1942), Däniker (1954), Greguss (1955) and others. In spite of the paucity of our knowledge of fossil species, we know much about the various forms of stems, leaves and the reproductive structures in the principal groups ; we have some knowledge of the periods in the past when they lived, and of their relative abundance. Our information is doubtless incomplete, but it provides much material for critical consideration, and the attempt to link up the data into a scheme showing the evolution of plant structure is a valid scientific discipline. While the suggestions of some authors seem speculative, the subject is worthy of close attention for it has led to the appreciation of some aspects of plant structure that may have been previously overlooked.

The details of the various schemes that have been proposed cannot be given here, but reference must be made to the papers of Prof. Lam, who has kept in touch with recent palaeobotanical discoveries and has considered the views of other writers on the subject. He has suggested a revised way of classifying the plant world, based on extinct as well as on living forms. A certain amount of agreement is to be found among the various writers on the general evolutionary trends in several groups, but, as may be expected, diverse views are held about the ancestry of the angiosperms.

Character Phylogeny.

Many botanists have made comparisons of the structures found in taxonomic groups of modern plants, with the object of discovering the probable evolutionary development of those structures ; such work generally depends on suppositions as to the form of the more primitive types. Character phylogeny has the same aim, but is based on the examination of stems, leaves or reproductive structures in groups of apparently related plants, taken in the historical sequence of their appearance in the fossil record. When all the known forms of a particular organ from successive horizons are taken into account, the general pattern of the changes that have taken place can generally be discerned. The types of change and their rates vary independently, and examples of the more primitive forms may persist for some time among more advanced types.

The photosynthetic organs of megaphyllous plants, being the parts most commonly preserved, present much material for this kind of study. The general sequence of changes is found to be, from a highly branched lateral shoot to a flat compound frond with small pinnules, then to structures in which pinnules and pinnae become more or less united by parenchymatous tissue forming the mesophyll, with the original branches, pinnae axes, etc. represented by the veins. Comparable changes appear to have taken place at different times in the ferns and the seed plants. Early in this century Lignier (1903) brought forward the hypothesis, based on the succession of the fossil forms that the fronds of ferns were derived from branch systems. More recently Zimmermann (1952), Emberger (1953), and others have dealt with similar series. It seems possible to regard most, if not all, of the changes in the form of fronds and leaves as due to mutations producing changes in the relative growth rates of the different parts of the organ. Zimmermann, who has discussed the question in several publications, considers that the changes have arisen by the action of several " elementary processes " among which he distinguishes (*a*) Overtopping, a process leading to a distinction between rachis and leaflets, pinnae and pinnules, etc. (*b*) Plantation, when the telomes and mesomes became arranged in one plane. (*c*) Syngenesis, where the telomes and mesomes became connected by parenchyma (forming mesophyll), or by their steles. (*d*) Reduction. (*e*) Incurvation, unequal growth on two opposite sides of the organ. (*f*) Longitudinal differentiation, usually affecting the extent of the other processes at different parts of a leafy structure. The different types of change are regarded as independent of one another.

There seems to be abundant evidence for such a theory from the fossils. It also obtains support from recent observations on the development of leaves in living dicotyledons (cf. Slade, 1957), and on the influence of chemical substances on leaf form. It is also probable that environmental conditions have played some part in causing, or selecting, changes in leaf form, which may also have been influenced by evolutionary changes in the stems and roots of the plants.

It is of some general interest to notice that the fossils seem to show a high probability that compound leaves are more primitive than simple leaves, and this may be applicable to the flowering plants. But large simple leaves with a reticulate venation appear in the fossil record towards the end of the Palaeozoic period.

Reproductive structures of successive periods may be usefully compared in a similar way to the comparison of leaves above mentioned. An outstanding example of such work has been provided by the researches of Prof. Florin (1938–45) on the Cordaitales and Coniferales. These have cleared up the long debated problem of the morphological interpretation of the female cones of the living conifers. Similar studies in other groups may well lead to results of comparable interest and value.

The Origin of the Angiosperms.

From the early days of the theory of Evolution the origin of the flowering plants has been one of its major problems. This group, now the largest, the most widespread, and the most diversified class of the higher land plants, is greatly different in structure and reproduction from all other living forms. Dicotyledons appeared in considerable numbers and variety in Upper Cretaceous times, and their evolution may well have continued at a rapid rate since that period. It is widely held that the fossil record throws no light on their Pre-cretaceous ancestors, but it is difficult to believe that no evidence bearing on their origin exists among the fossil floras that have been discovered. It is quite possible that being essentially plants of dry lands (Axelrod, 1952) they did not grow in places where their remains had any chance of being preserved, or that the areas in which they originated have not yet been thoroughly searched. But we may have found the remains of their ancestors, or of allied types, without recognizing them. The writer believes that this may be due in part to the persistence of the old ideas on original plant form based on the classical morphology of Goethe, and in which the parts of the flower had to be either leaves or stems. These concepts, which cannot be applied to evolutionary studies, made botanists think that they knew what was the form of the early flowering plants, and they made a completely unsuccessful search for fossils which realized their ideas.

The leaves of the dicotyledons have a characteristic form, but apart from two isolated specimens from the Jurassic rocks, the only species with leaves of this type which he called *Furcula granulifera* was found by Prof. Harris (1932) in East Greenland in Rhaetic rocks. We now know, however, that the veins in many living forms show a simple closed reticulum at an early stage in their development ; a type of venation which was present in many earlier forms, such as *Glossopteris*, *Anthophyopsis*, and *Caytonia*. The Mesozoic and some Palaeozoic gymnosperms had inflorescences with groups of reproductive organs terminating their branches. It is easy to interpret the flowers of the angiosperms by reference to these, and it seems more logical to do so than to regard the floral organs as a series of modified leaves, a type of structure which is quite unknown among the plants of the past. The fossil record of reproductive branches gives strong support to the view that bracts and bracteoles, sepals and petals are new structures due to changes in the growth of the reproductive axes and not modifications of pre-existing leaves. These ideas may form the basis of a re-assessment of the living angiosperms, and a new search for the characters correlated with structures known to be primitive. The work of Sporne (1949) on these lines may well show that the origin of the flowering plants is not so mysterious as was previously thought.

Apart from the search for primitive angiosperms, palaeobotanical work of great importance has been carried out on the angiosperm remains from the Upper Cretaceous and Tertiary rocks. In Darwin's time the identification of genera was mainly based on the identification of leaf impressions, and many of the names given were open to criticism. Now, by the patient labours of many investigators, we have evidence from fruits, seeds, pollen grains and some remains of flowers, as well as from well-preserved leaf remains. The pioneer work of Clement and Eleanor Reid on ancient fruits and seeds, has been well followed up in Europe, while the studies of E. W. Berry and Prof. Chaney and others on leaf remains in America have been very valuable in disclosing much of the later history of the angiosperms. This work, which is still going on, will tell us much about the evolution of the group.

Palaeobotany and Natural Selection.

The study of the past history of plant life might be expected to furnish some evidence of the mechanism of evolution and especially of the role of natural selection in the origin of species. It must, however, be remembered that plants differ greatly from animals in their structure and their mode of life. Anatomically they are very simple when compared with most animals; apart from the fungi, their nutrition is very uniform in character, they are fixed in the soil from which they draw water and mineral salts, all of them need suitable illumination and temperature for growth. The competition for existence is different from that in the animal world, where food chains of a complicated nature may determine the perpetuation or extinction of a race.

In the past many botanists have tended to regard structural characters as the all important factors determining the viability of a plant species, and have looked on all variation in form as due to natural selection. There were so many varieties in floral structure which seemed like adaptations for pollination by insects or birds; there were different types of fruit affecting their seed dispersal, and so evolution was considered as mainly a question of structural change. But few of those who discussed evolutionary problems were acquainted with the physiology of plant growth, or had studied the ways in which it is affected by environmental conditions, as shown by observations on species in the field or under cultivation. Thus the importance of the internal biochemical constitution of the plant was overlooked.

In nature competition between individuals and species undoubtedly exists. In many places species are seen with structural characters apparently related to their environment, such as succulence, but they often grow alongside plants without any such modifications of structure, moreover succulence may have originated from internal biochemical changes. More important than features of shape and structure is the water balance of a species, the optimum, maximum and minimum temperatures for growth and flowering, its illumination needs for vegetative growth and for flowering, the rate of its reproductive cycle. Thus it is not unlikely that biochemical changes arising in the nucleus, affecting the enzyme systems in the plant and possibly produced by cosmic ray bombardment, may be the real cause of the appearance of new varieties or species, and that visible morphological change may be often a secondary result. Physiological changes may become fixed by natural selection, especially when the species is subjected to climatic changes affecting its habitat. If this view has any validity we could scarcely expect to obtain any information about the origin of variations or the process of natural selection from the study of fossil plants. But this study shows that considerable changes in the vegetation of all parts of the earth often took place in the past, and these were associated with climatic fluctuations.

An interesting example of the relation between climate and structure is furnished by the Upper Palaeozoic Lepidodendrales. These plants were very abundant in the swamps of the Coal Measure period and many species referable to several genera had appeared. Their anatomical structure, which is very fully known, had become highly specialized for their mode of life. They formed trees of considerable size, with many leafy branches, but the stems and leaves contained very little water-conducting tissue. On the other hand they had a very large bulk of aerating tissue, essential for the growth of their Stigmarian axes and rootlets, which stood in water or anaerobic mud. This tissue filled a large part of the stems, it communicated with the rootlets below, and with both the mesophyll of the leaves and with the outside air above. When, at the close of the Carboniferous period, the swamps and lakes of the coal basins dried up, plants with such structure had little chance of survival and they became almost extinct. Only one small unbranched type, *Pleuromeia*, seems to have survived into Triassic times as a last and rare remnant of a large group.

There is geological evidence of frequent climatic variations and of changes in the distribution of land and water in past times. When these changes occurred some land plants were doubtless able to migrate to habitats where the soil, rainfall and temperature were suitable, although their light requirements may have limited their movements towards or away from the equator of the period. The information we now have about the effects of the climatic fluctuations in Quaternary times on the survival and distribution of species, provides an example of the type of change which has taken place constantly over the many millions of years of plant growth on the earth. Thus the great glacial period in the Southern Hemisphere at the close of Palaeozoic times must have had wide effects on the flora. After its maximum very large tracts of land were probably left as open habitats for plant growth, and for a long time the vegetation seems to have been sparse, although conditions were probably favourable for the establishment and preservation of species. It may be that this area provided the conditions favouring the rapid evolution and spread of the flowering plants. In fact a few remains of structures resembling the flowers of angiosperms have been found in the Triassic rocks of South Africa.

It is, of course, possible to point to different structures found among fossil floras and to claim with some degree of possibility that they originated through natural selection. The tightly closed cones found in Cretaceous times may have been responsible for the development and spread of the Abietineae. The fleshy, berry-like fruits of the Caytoniales with their many small stony seeds may have favoured the spread of these plants during the Jurassic period, when birds and small mammals were present to feed upon them. The Bennettitales in Lower Cretaceous times became much dwarfed, with their " flower " buds almost buried amid an armour of leaf bases, probably related to a gradual climatic dessication. But neither the Caytonias nor the Cycadeoideas seem to have survived beyond Lower Cretaceous times.

The changes in frond form in the ferns and pteridosperms that have been mentioned in an earlier section, might also be ascribed to the natural selection of variations tending to produce a more efficient photosynthetic organ. Although selection may account for the disappearance of some of the earlier frond forms, the idea can scarcely be applied to the fully expanded bi- and tripinnate types, such as are seen to-day in the ubiquitous *Pteridium aquilinum*. The formation and increase of auxins influencing the development of the growing points of the stems and fronds provides a more likely reason for the changes from a highly compound to a more simple form of leaf, than the selection of a less dissected form that had arisen by a chance variation.

Fossil Plants and Geographical Distribution.

The theory of Evolution involved the view that each species was first produced within a single region (Darwin, 1888, p. 320). It was therefore necessary for Darwin to consider the present discontinuous distribution of species, and to extend this to the cases where different species of one genus occupied widely separated areas. Two chapters of the *Origin of Species* were devoted to the discussion of Geographical Distribution, in which special attention was paid to plants. The theory was put forward that discontinuous distribution was mainly due to the migration of plants in former periods when climatic conditions changed and were different from those of the present day. The possibility of changes occurring in specific characters during such migrations was envisaged.

The argument was developed (*Origin*, p. 330) from the explanation given by Edward Forbes of " the former influence of the glacial climate on the distribution of the inhabitants of Europe ". At the period of maximum glaciation much of Europe and North America, now having a temperate climate, were thought to be inhabited by an arctic flora and fauna, some of whose members ascended the higher mountains and remained there when the climate was ameliorated. This view has long been accepted as the most probable explanation of the discontinuous distribution of certain arctic-alpine species, but it is only in recent years that unquestionable evidence has been found to prove that such migration is an historical fact.

The researches of Clement Reid published in *The Origin of the British Flora* (1899) began the investigation of the remains of Quaternary plants, which in the last thirty years has been actively pursued by many workers in different countries. Dr. Godwin, one of the leaders in this work, has shown in his *History of the British Flora* (1956) that we have ample evidence from pollen, seeds and other macroscopic remains of the widespread occurrence of arctic species in England after the retreat of the ice. Much is known of the changes in climate, from the last glaciation to-day, and of the succession of species in the vegetation; we also have some evidence of the composition of the flora of the previous interglacial period.

After giving an account of the theory of Forbes on arctic-alpine species, Darwin went on to consider the possibility that early in the Pliocene period, when the climate was warmer, plants now growing in the temperate regions of the Old and New World extended northwards and were perhaps circumpolar. He thought that towards the end of the Pliocene, when the climate became colder, these plants would probably have retreated southwards, and so become separated in two distinct areas. He was strongly inclined to extend this view to some still earlier and still warmer period, when other plants with a circumpolar distribution may have extended southwards to those regions where we now see their descendants, mostly in a modified condition.

Recent research on the fossil plants from the Tertiary rocks has shown that these suppositions also are in the main historically justified. In 1920 Mrs. Reid provided evidence of a southward migration of the floras in Pliocene times resulting in floristic differences in different regions. Her conclusions were drawn from the collections of fossil seeds from different horizons in Western Europe. A comparison of the species identified showed that early in the period the flora of Western Europe contained a considerable number of species (64 per cent of the total) which are now extinct in Europe but are found in mountainous regions in North America and China. As time went on the percentage of such species diminished, suggesting a retreat with the onset of colder conditions. In Europe this retreat was blocked by the east-west mountain ranges and the Mediterranean Sea and many species perished, while, in North America and China, passages to warmer regions were open, and at a later date many forms were able to return northwards to the areas in which they still grow.

Further research has provided evidence of an earlier southward migration in Oligocene or Miocene times. The Eocene floras of Southern England have been shown by Mrs. Reid & Miss Chandler (1933) to contain many forms closely allied to species now growing in the tropical rain forests of the Malayan region. Similar vegetation was found in North America, while further to the north there was temperate woodland extending to Greenland and Spitzbergen, and probably circumpolar. The evidence, especially that found in North America by Prof. Chaney (1940) and his collaborators, indicates that as the climate became cooler, and probably drier, the temperate woodland plants moved southwards, and probably xerophyllous woodland, savanna and grassland became extensive. Axelrod (1952*b*) has summarized the probabilities of dispersal during this period. Further evidence of migrations in North America has been provided by a statistical analysis of the floristic composition of the fossil remains from Upper Cretaceous to Pliocene times by Dr. Barghoorn (1951). This shows a steady change during the period in the number of genera with representatives in the existing flora of the geographic region of the deposit, and in the number of exotic genera. He also provided data showing the relative numbers of unidentified, "extinct", or form-genera present at each stage; this may perhaps give some indication of the morphological changes that occurred during the period, for it seems unlikely that the high percentage of unidentified forms in the earlier floras is entirely due to the extinction of genera.

Apart from the problems which Darwin considered, palaeobotanical research has disclosed many other difficult questions relating to past geographical distribution, on which valuable data were collected and presented by Seward in his *Plant Life through the Ages* (1931). Some of these have given rise to considerable discussion, such as the problem of the discontinuous distribution of the Gondwana flora of Late Palaeozoic and Early Mesozoic times. The remarkable similarities between the representatives of this flora in India, South Africa, Australia and South America seem inexplicable if the continental masses and ocean basins had in Late Palaeozoic times the positions which they occupy to-day.

Our fossil floras also supply evidence of many wide ranging forms in past times, such as the occurrence of *Lepidopteris* in the Triassic rocks of East Greenland, Sweden and South Africa. We may thus conclude that at all periods land plants have migrated over long distances, and that Darwin's suggestions, long regarded as providing a satisfactory theory, now have the status of proved historical fact.

Summary and Conclusion.

The study of fossil plants during recent years has given a much wider and more comprehensive view of the vegetation of the past, extending back to the Silurian period. It has shown that many groups of the higher plants formerly existed whose reproductive features were very different from those of any living types, though in their basic units they are often somewhat similar. The evidence suggests the derivation of the higher land-plants from five or six ancient types, although nothing is really known about the possible connections of these ancestral forms.

Modern technical methods of treating the fossil remains, and systematic collecting by trained botanists, have rendered our knowledge more precise and reliable.

Owing to the comparative rarity of conditions favouring the preservation of plants as fossils, no long series of forms have been found from which the evolutionary history of species or genera can be determined. The general historical trends in certain large groups, and in the characters of some of the organs within those groups may be inferred from the fossil evidence.

The reproductive branches of most of the higher plants show increasing complexity with the passage of time. The fossil record suggests that this was often due to the formation of new structures in the region between the site of reproductive activity and that of purely vegetative growth. These new structures (cupules, bracts, etc.) do not seem to be, in the historical sense, modifications of pre-existing organs.

No evidence has been obtained as to the way in which species have originated. Darwin's views on the migration of plants in the Tertiary and Quaternary periods have been shown by direct evidence to be fully justified. It seems certain that similar migrations have take place repeatedly in the distant past.

The idealistic concepts of plant form laid down by botanists under the influence of the belief in special creation appear to have no historical foundations. Many early plants had no real leaves or roots, and there is good evidence that fronds and large leaves have evolved from branch systems. Hence the distinction between branches and leaves, which has played in the past such an important part in the discussion of evolutionary problems, has no fundamental significance. The belief that the sporangia of all the higher plants were originally borne on fertile leaves, or sporophylls, is without material foundation.

The fossil record now available provides the groundwork for a new and materialistic philosophy of plant structure. It shows that the idealistic view of plant form, derived from the ancients, is not applicable to the evolutionary point of view. It indicates, as Dr. Agnes Arber (1950) has ably shown, that a philosophical distinction must be made between idealistic morphology and materialistic (evolutionary) morphology, although both are valid modes of approaching the study of plant form. But during the past century the two view points have been confused, and this has resulted in much fallacious reasoning.

It seems likely that the investigation of fossil plants will influence the study of plant evolution most strongly by showing that a completely new approach to the problems of plant form must be adopted. In this almost all aspects of botanical study should be integrated with the object of discovering how plants have come to be organisms such as we now see them.

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THE EVOLUTION OF FLORAS WITH SPECIAL REFERENCE TO THOSE OF THE BALKAN PENINSULA

By W. B. TURRILL, F.R.S.

Being the HOOKER LECTURE delivered to the Linnean Society on 17 *April* 1958.

Introduction.

The Hooker Lecture commemorates the life and work of Sir Joseph Dalton Hooker (1817–1911). It seemed appropriate to combine in this year's lecture two subjects that were of primary interest to Hooker and to the advance of which he contributed so much, namely organic evolution and plant geography. For those who regard taxonomy synthetically it is easier to combine than to separate these subjects, and the difficulty has been to compress the wealth of material into one lecture. Some artificial limitations are imposed and several important matters are ignored or barely mentioned partly because of lack of time and partly because they are outside my personal experience. Most of the illustrations are taken from the floras of the Balkan Peninsula and some other areas of the Mediterranean and Central European Regions. Further, only the seed-bearing plants are considered.

In botany, evolution may refer to the origin and development of (*a*) species and other taxa, (*b*) vegetation, (*c*) floras. It is often not necessary to distinguish these usages of the term and it is impossible adequately to consider any one without frequent reference to the others.

The orthodox taxonomic units, and especially species, form the basis of ecological and phytogeographical studies. It is all to the good that there should be constant criticism of taxonomic schemes and methods, so long as the critics are well informed and have their facts correct, a condition that does not always obtain. It remains, that no generally useful scheme has yet been published and tested to replace the hierarchical classification into families, genera, and species and that, on the whole, the work of plant taxonomists has been found adequate for ecologists, phytogeographers, cytogeneticists, and other specialists. The main difficulty in applying a classification linked with a nomenclature that in theory should be static is that when species (or other taxa) are studied as populations they are found not to be static but changing. Whether classification and nomenclature can be given a degree of elasticity to meet this behaviour of plants, especially when the changes are of the nature of long-range evolution, is a problem that will have to be considered when further researches on the composition and behaviour of taxa are available. Changes in vegetation have two aspects, the successional change, culminating in a climax that is stable relative to the earlier stages of a sere, and long range change most often associated with secular changes of climate. The former is, or may be, frequently repetitive, the latter is often, if not always, unique and can correctly be termed evolution.

The word " flora " has several dictionary definitions. Here we use it to mean the sum total of seed-bearing plants classified into taxa and occurring in a given geographical area. When a geographical area is subdivided the flora is subdivided. One can speak of the flora of the Mediterranean Basin and of the flora of southern France, of Cyprus, etc., without ambiguity when the sum totals of the plants of such areas are intended. Some care is needed in the use of phrases such as "the Mediterranean flora in Serbia ", meaning the occurrence in Serbia of those species whose ranges are centred in the geographical Mediterranean Basin (or Region).

Description, Classification, Causation.

There are three essential stages in the study of evolution of floras : description, classification, causation. It is sometimes considered very up-to-date to give a low estimate to descriptive work in taxonomy, ecology, or phytogeography. This is unfortumate and, in my opinion, can only result in wrong conclusions being reached. Description is only one stage in phytogeographical research, as it is in any other branch of biology, and it is an art or craft as well as a fundamental method of science. Description in plant geography has two functions : it is, or may be, of use in itself and it is an essential preliminary to the study of causes and therefore of an understanding of the origin of floras. The use of good descriptions in themselves was strongly impressed on me during the second world war when I was working for two service departments needing information concerning the flora and vegetation of certain areas where operations were contemplated. I cannot give details, but the authorities wanted exact information concerning such matters as composition of flora, nature of vegetation, penetrability, density of cover, seasonal behaviour; food values, and so on. They wanted accurate and detailed descriptions of what was there, while classification and theory of causes or origins, what we might consider scientific explanations, were not of the slightest interest to them. However, to us, descriptions are the raw facts so pictured as to be complete for our purposes, comparable one with another, and classifiable.

The second stage is that of classification. The different floral units have to be named or otherwise designated, diagnosed, and then related one to another in a logical classification. As with taxa, one can have special and general classifications. The former are made by using one criterion or at most very few criteria and are to a high degree " artificial ", while, in making the latter as many criteria as possible are used and the resulting classification is based on a maximum number of correlations and to this extent is less abstract. The criteria that may be used are extremely varied and it is part of the purpose of this lecture to investigate them. From our point of view the importance of a classification of floristic units is that the determination of their origins will be made easier the more general and valid is the classification used. No term for biogeographical or for floristic units has been found comparable with taxon (pl. taxa) now in general use for taxonomic units of any status. The word chorion (pl. choria) is therefore proposed here with the advice of Mr. N. Y. Sandwith. One can make a botanical restriction by using phytochorion (pl. phytochoria) and a zoological one by using zoochorion (pl. zoochoria).

Following description and classification there is the stage of causation. How have choria come into being ? What are the causes of their genesis ? How have they developed and what has determined their particular development? How far are they now stable and how far are they changing and if changes are occurring what causes them or controls them ?

The three stages of description, classification, and causation follow one another in logical theory. In practice, one collects data for all three as opportunity offers for any piece of research and in discussing methods here logical methodology will not be stressed and will at times be ignored.

Plant geography as a whole is a highly synthetic subject and data from many branches of knowledge have to be considered. As with every other branch of botany it has to be based on taxonomy and this dependence cannot be too often stressed, though it is frequently ignored or insufficiently emphasized in many text-books and other publications. The units of a flora, of any phytochorion, are the taxonomic components or taxa. These are determined by the taxonomist as such and are then accepted by the phytogeographer. That the latter has often to be his own taxonomist has some advantages though it may increase the danger of *circulus in definiendo*, that the taxonomic units be not defined on grounds entirely independent of ranges. If we acknowledge the taxonomic basis of plant geography and, therefore, of any study of the origin of floras, the following are some of the data which must be used in our studies. There must be accurate determination of the actual composition of the flora of a stated area. The geographical boundaries must be clearly stated and strictly adhered to for any given piece of research. There will often be a taxonomic limitation in that the phytochorion is taken to include only the Spermatophyta or, at most, only the vascular plants, though ideally it should include all plant groups. The composition of the phytochorion is determined by field studies, by consulting herbaria, and by abstraction from literature. Difficulties frequently occur. Time for field work may be limited, herbarium material is all too often inadequate, and published records are not invariably reliable or unambiguous. Fortunately the methods can often be used to check one another. Accepted records are best made on a loose-leaved system, sorted, checked and counter-checked, and can finally be plotted on maps and used in various ways for statistical analysis and synthesis. The degree of refinement in mapping and in statistical treatment varies with the size of the area and with the details of the aims of the research. Here reference need only be made to the symposium on this subject published in 1954 by the Royal Geographical Society (The cartographical presentation of biological distributions). For the British Isles, the advantages of range mapping on the grid system have been very fully discussed and mapping is proceeding for all the seed plants of the British flora. One has to note that money is not available for detailed mapping at all comparable to this for areas such as the Balkan Peninsula.

Analysis of a phytochorion other than by detailed mapping is not only possible but imperative if the composition, and finally the classification and development, of the phytochorion are to be understood. The advantage of filing records on cards is evident in such analyses. The component taxa can then be readily classified in many special ways and statistics worked out for ecological distributions, correlations with climatic, edaphic, and biotic factors, flowering periods, life-forms, altitude, etc. Such special classifications are of very great use in preparing a general classification of the phytochoria of an area and in determining their origins and causations.

It is important to emphasize that classification of phytochoria must be on the basis of the plant life only. They must not be delimited by non-botanical criteria. We must not, for example, divide the Balkan Peninsula on climatic criteria or on physiographical features and delimit phytochoria to fit in with climatic zones or with geographical peculiarities. Valid correlations can only be obtained when the variables are determined independently. Phytogeographers have not always been free from this error and with well marked climatic or altitudinal zonation, for example, there is always the temptation to anticipate botanical results by short cuts, though these may to some extent invalidate the results.

The plant life of a phytochorion consists of systematic units or taxa which are more or less obviously and definitely grouped into communities of vegetation. Phytogeography is not sharply marked off from plant ecology, and though difference in floristic composition is generally regarded as the first criterion for separating phytochoria, vegetational differances are of great importance and ecological distribution has, so to speak, one advantage over ranges as usually recorded or mapped. A plant community is often defined by dominant or at least abundant items, either taxa or life-forms, while ranges usually do not record whether a taxon is common or rare. Thus a single occurrence will result in a whole vice-county or a grid square being blacked. There are of course devices for reducing the disadvantage of lumping together mere records of floristic occurrences, but adequate data are not always available for using them. The communities of vegetation, and particularly of the climax vegetation may give better correlations with non-botanical variables acting at the present time, such as climate or soil, than do merely mapped ranges of taxa. The subject is a complex one and is well illustrated by the extensions of Mediterranean elements in the Balkan Peninsula even into parts well beyond the limits of the Mediterranean vegetation proper and the Mediterranean climatic zone. In the end, the phytogeographer has to use all possible criteria, to balance up the data, and often to recognize wide transition belts.

So far we have considered the actual plant life as flora and as vegetation. If we wish to consider its origins we have to find out as much as possible of its past history.

Indirect evidence may be given by details of ranges and distributions. The most direct evidence is palaeobotanical. The value of fossils in the study of the history of a flora is nowhere better illustrated than in the British Flora as shown in Godwin's recent book *The History of the British Flora*, Cambridge 1956, and by the researches of Mr. and Mrs. Clement Reid and Miss Chandler. Work in North America by Chaney, Mason, and others clearly supports the view that much light is thrown on the development of floras by palaeobotanical data. Like all other facts these need careful checking and interpretation in correlation with all other evidence. Unfortunately, for the Balkan Peninsula relatively few deposits of fossil plants have been critically examined. In the south and west of this area climatic and other conditions have not favoured the accumulation of peat so that the study of post-Tertiary pollen is limited. Published determinations of plant fossils cannot all be accepted. Examination of the material at the British Museum (Natural History) from Skyros determined by Gunnar Anderson as *Rhododendron ponticum* L. led me to reject the record. However, there is no doubt that even for the Balkan Peninsula the fossil plant deposits awaiting examination by modern methods could give most valuable information regarding the history of the floras.

Palaeobotany is not the only help given by geology to the plant geographer. Any facts regarding past climates and climatic changes are of great interest to him. Straightforward geology is often of great importance and especially information regarding changes in land and sea relationships and in altitude. The plant geographer must never put forward hypotheses that conflict with well-established geological conclusions. It may even be undesirable for him to accept geological hypotheses that are in dispute amongst specialists however much they may appear to favour some pet hypothesis of his own.

Origins and Developments of Floras.

We come now to the origins and developments of existing floras as we can study them by the evidences just outlined. The facts we have are always incomplete in any general sense, and we have from time to time to make decisions that can only be tentative. I am limiting what I have to say here to spermatophytic floras and mainly to the angiosperms. Even so one cannot say when or where or from what such floras originated from the beginning. The origin or origins of the flowering plants from any pre-existing group or groups is still so hypothetical that it is best regarded as unknown for our purposes. They may go back to the Triassic or even Permian but the evidence available is that the flowering plants did not markedly influence most floras or dominate most plant communities till the Lower Cretaceous. Analysis of existing ranges and what is known of fossil plant deposits shows clearly that floras are not static. Changes in them may be gradual or catastrophic. Climate, a complex aggregate of factors, is the main limiting factor, but not the only one. The idea of tolerance to the sum-total of factors is often valuable in considering the range and evolution of a taxon or of a phytochorion, but it is frequently more illuminating to take an opposite view and to find out the limiting factor or factors to increase of range. One may, for instance, even say that a given taxon can live anywhere until it encounters some limiting factor or conditions. Especially in trying to determine causes of floristic evolution the limiting factor view is often more helpful than that of tolerance even if one accepts that they are only different viewpoints of the same phenomenon. For a phytochorion there is under existing conditions a relative climax, as there is for vegetation, but we are here concerned less with short term stabilization than with long term evolutionary changes. It is possible to classify these into two groups: *in situ* development and changes due to immigration and emigration. If one does this rigidly there has to be some repetition—or some criss-crossing in the classification. For example, hybridization may be a factor involving only elements developed within a phytochorion or it may involve immigrants. One may also ask " when does an immigrant become a native ?". It is, however, important to recognize that *in situ* development can be important and that it raises problems in itself that often contrast with those of immigration.

In situ *Development of Floras.*

In situ development of a flora takes place by the mutations and hybridization of taxa and by their dying out. It has been urged that in the early history of angiosperms mutations were large and infrequent and now are smaller and more frequent. Terms like " large " and " small " in such a context need definition or at least adequate illustration. One can only say that variations with a genetic basis, reasonably assumed to be of mutational origin, are found from time to time in existing taxa and are apparently of very varying degrees of importance to survival of the individuals having them and of conspicuousness to the botanist. They vary also in the taxonomic value that has been assigned to the characters involved. It is probable that in wild plants, as in plants cultivated under control for genetical research, the majority of mutations are disadvantageous, but " advantage " or " disadvantage " are sometimes difficult to determine. Since it appears that mutations are of all degrees from one extreme of very considerable advantage to another of very great disadvantage (even to lethality), it would appear that some mutations are more or less neutral, and one has to remember also that a change in environment may swing a mutation from the advantageous to the disadvantageous category. The subject is made still more complex by the fact that genes are often, if not always, pleiotropic. Examples of variations within species are numerous. My own experience, limited though it be, makes me bold to say that species as usually accepted in taxonomy in many genera are much more variable genetically than is generally realized and certainly than is stated in many published accounts. This is true for such species as *Silene maritima* With., *Silene vulgaris* Garcke, *Ranunculus ficaria* L., *Saxifraga granulata* L., and others we have studied experimentally and with some intensity. It is true for some species of *Fritillaria* especially in the Nearer East and for species of *Jasminum* in Tropical Africa. There is often a wealth of variation within a taxonomic species. If this be geographically restricted subspecies may be recognized, if it be ecologically restricted in a narrower manner ecotypes may be abstracted. How far names should be given to paramorphs is a practical question and I would merely express an opinion that they should only be given when needed to serve some definite scientific or economic purpose or where the variant is exceptionally clear-cut. We found it impracticable to give names to all the variants we studied in the bladder campions but to discuss our difficulties in this group would take us too far from our present subject. A few examples of paramorphs within my ken will illustrate their morphological diversity. *Pulicaria dysenterica* Gaertn. var. *hubbardii* Turrill was found in a colony of the species near Islip in Oxfordshire. It has remained true to its diagnostic characters for fifteen years and " comes true " from seed. The male variant of *Ranunculus acris* L. has, to our knowledge, only been found once, in Cumberland, but we have proved it to have a genetic basis and have raised numerous plants in F_2 and subsequent generations of which it was an original parent. As a minor variation I would mention *Berteroa orbiculata* var. *glabra* Turrill with glabrous pods which we found on one of the Mulyani Islands in the Aegean and near Simopetra on Athos. *Silene subconica* Friv. var. *grisebachii* Davidoff was originally found and described on the sandy shores of western Thrace by Davidoff. We have received excellent material more recently collected by H. G. Tedd. The elongated petal claws of this variant are very striking. One British example of the common bladder campion is worth mention since it suggests a " large " mutation in the taxonomic sense though disadvantageous by itself. This was a plant with the calyces split into segments more or less corresponding to sepals. The genus *Silene* is the name genus of the subfamily Silenoideae which is characterized by a gamosepalous calyx in contrast with the subfamily Alsinoideae with a polysepalous calyx. The mutant, from Surrey, should technically be moved from one subfamily of Caryophyllaceae to another. It was recessive to the normal condition. One could extend examples almost indefinitely, but it is perhaps worth stating that taxonomists are more acquainted with the extent of variation in wild taxa than are most geneticists and can accept that gene mutations may be and often are the basic raw material for the *in situ* evolution of floras.

Mutations can result in convergence or even in polytopy or " near polytopy ". Briquet argued for polytopy in his analysis of the flora of Corsica. Interesting examples of convergence or " near polytopy " occur in the genus *Silene*. *Silene maritima* does not occur in the Balkan Peninsula or, in our experience, in the Mediterranean Basin. *Silene vulgaris*, however, is a common and exceedingly variable species. In Dalmatia it has developed a variant, var. *reiseri* (K. Maly), which has various characters of morphology and ecology recalling those of *S. maritima*. Again, *S. vulgaris* subsp. *alpina* (Lam.) Schinz et Kell, has a fairly wide range in the European Alps and extends discontinuously in the mountains in the western parts of the Balkan Peninsula at least as far south as Bosnia. A very similar variant also occurs in the Balearic Islands and was almost certainly of independent origin from the Alpine plant.

Changes in the chromosomes, whether inversions or other structural changes or multiplication or loss, have received considerable attention in recent years from cytogeneticists. In that they often result in genetical isolation they are of particular concern to the phytogeographer but the vast majority of plant species of wild floras have not yet been adequately examined cytogenetically and it is difficult to generalize on the importance of cytogenetical isolation in the origin of floras. There are, amongst plants, what appear to be surprising exceptions to any general rule that taxonomically nearly related species will hybridize while more distantly related ones will not. *Geum urbanum* L. amd *Geum rivale* L. hybridize freely, so do many species of *Dianthus* from the Balkan Peninsula and elsewhere. There is also no exact correlation between time or space factors in evolution and cytogenetical isolation. Thus, *Platanus orientalis* L. from the Nearer East is fertile with *P. occidentalis* from south-eastern North America, as witness the London plane.

Polyploidy is not only of importance to plant geography in the formation of taxa, but can directly throw light on the origin of phytochoria. Polyploids originate from diploids, or, at least, from lower polyploids. Consequently diploids are anterior to polyploids though it has to be investigated carefully whether they have originated *in situ* or have immigrated into a given phytochorion. The study of polyploidy in relation to the origin of floras is in its infancy and one has to be cautious in making wide generalizations. Relatively few taxa have been adequately examined cytologically in wild material of known origin and the correlation of polyploidy with taxonomy is in an unsatisfactory state. It is certain that some polyploids show ecotype differences from their parental diploids. There is also evidence that some polyploids can withstand more extreme environmental conditions than the diploids from which it is assumed they were derived, but this is not true for all polyploids. There are distinctions to be made between autopolyploids and allopolyploids and physiological robustness of phenotypes, reproductive capacity, vegetative multiplication, and other features of behaviour have also to be considered. It has been stated that " perhaps the safest generalization that can be made about polyploids is that they are most numerous in regions that have only recently been open to colonization by plants or that have undergone great changes in their floras in recent times " (Stebbins, *Amer. Nat.*, **76,** 36 : 1942).

Mutations, genic or chromosomal, provide new basic characters, but hybridization, by leading to new combinations of genes, may also result in new " characters " some of which may become fixed in the Mendelian sense of homozygotes or by allopolyploidy. While Lotsy, for example in a famous lecture delivered in 1914 to this Society, probably over-emphasized the importance of hybridization in evolution, it has played a part in the evolution of floras. This is particularly true when potentially interfertile taxa extend their ranges so as to overlap. It may be that one immigrant comes within pollinating distance of a species already a constituent of a phytochorion, as

Centaurea jacea L. entering chalk or limestone grassland in southern England and mixing with *C. nemoralis* Jord. It may be that altered ecological conditions allow the spread towards one another of species previously isolated geographically, as appears to have happened in such genera as *Dianthus*, *Asperula*, and *Thymus* in the Balkan Peninsula, and that when the ranges meet hybridization occurs with the production of hybrid swarms if there are no, or no strong, sterility factors involved. The distinction between *in situ* development and development by immigration is here blurred if it does not break down completely. There is no doubt that introgression, to use Anderson's term, plays a part in the development of floras.

Changes in floristic composition are brought about not only by the appearance of new taxa but also by the dying out of existing ones. The causes of this are usually obscure. Comparisons between life histories of indviduals and duration of taxa can be misleading. A good deal has been written about senescence of species. There is little, if any, clear cut evidence of loss of vitality in species as a whole due to mere old age degeneration, whether this be measured in terms of vegetative vigour or of reproductive capacity. For reasons most often not understood there may be loss of variability in a species as a whole, that is depauperization of its biotypes. Environmental changes are the chief causes of extinction of species in a given phytochorion but this is correlated with two internal factors : the range of plasticity or the capacity to react to environmental changes and the potentiality for producing mutations. A species able to react favourably as a whole to climatic or other changes or with some biotypes capable of such reaction is the more likely to survive. It is accepted that some environmental factors increase mutation rate and this may occasionally be a factor in survival with change in a taxon. Environmental changes may favour the extension of range of an " old " species. Amongst the ancient relict elements in the Balkan Peninsula are the genera *Haberlea* and *Ramonda* of the Gesneriaceae. *Haberlea rhodopensis* Friv. is a plant of semi-shaded rock crevices and similar habitats. It appears to be extending its range in South Bulgaria and perhaps in western Thrace, in correlation with the opening up of montane and lower high mountain areas in the early degeneration stages following exploitation, by human activity, of what were closed forests, and resultant partial exposure of rocks. Certainly it was flourishing and spreading on rock exposure along newly-formed paths and roads in parts of the Rodopes in 1926. One has always to remember that the terms " old ", " young ", and even " relict " are often used relative to the flora and area with which one is dealing and not always or necessarily to the whole range of a taxon. The relict area is the remains of a larger area that was attained under earlier conditions of colonization different from those now predominating in the locality. A relict species is often in ecological disharmony, and, not being well suited in any of its biotypes to its present environment, is retrogressing. If there be addition to the biotypes by mutation, or by immigration (perhaps with hybridization), or if the environment changes, the retrogression may be stopped and even replaced by progression. Continuity or discontinuity of range may be suggestive in determining relative age. In general, the higher the status of the taxon showing discontinuity the older is that discontinuity and the greater the distance between occurrences the longer the discontinuity has lasted. There are exceptions to this generalization and to the further hypothesis that a taxon with a highly discontinuous range is older than one, even within the same taxonomic circle, with a continuous range.

That species do die out is, of course, certain from palaeobotanical evidence but we are very ignorant as to causes. It might indeed be noted that the subject of " death" amongst plants in nature has never been investigated extensively as a subject in its own right. It requires systematic study quantitatively and qualitatively. Physiology, pathology, competition, long range and short range changes in physical environmental characters, and various other factors are involved and individuals, of or within populations, and taxa will require different methods of study which, however, should be linked together.

Immigration and Emigration.

We turn now to a brief consideration of development of floras due to geographical movement of taxa, that is to immigration into and emigration from phytochoria. The botanical problems of " movement " of species (or other taxa) are dependent on dispersal of disseminules or diaspores, whether in the form of spores, seeds, or vegetative propagules. Apart from some of the thallophytic cryptogams, there is very rarely long distance change of site of whole mature plant bodies. In general, vascular plants are fixed in contrast with the mobility of many animals. There is both migration of taxa as single units and of masses of taxa in vegetation spread. The former may most often be more rapid than the latter. The efficiency of dispersal mechanisms has been much debated. It is very rarely 100 per cent perfect ; there is nearly always an enormous wastage of disseminules. For short distances, without effective barriers, it is generally agreed that it keeps a species in existence when and where there are no limiting factors to establishment. Phytogeographically the problems concern long-range dispersal especially over what are now seas, oceans, deserts, mountain areas, or extensive closed plant communities. There is very little direct evidence of long-distance dispersal of viable disseminules by agents other than ocean currents (for a limited number of littoral plants) and man. There is however some, and a reason there is not more may well be that the subject has not been properly investigated by teamwork involving ornithologists, meteorologists, and aeronautical experts amongst others, supervised by botanists. Here is a subject that would bring space travel down to earth, or a least to our own atmosphere. The matter was discussed at some length in the account of Sir Joseph Hooker's phytogeographical researches I published under the title of *Pioneer Plant Geography* and in my presidential address to the British Ecological Society (*Journ. Ecol.*, **39** : 205.227 : 1951). Personally, I cannot dismiss the probability that effective long distance dispersal occasionally occurs over considerable barriers. These barriers have a tremendous selective influence and disseminules very rarely get over them or establish themselves in new areas far from their homelands, but time is long and chance is patient and it was statistically highly improbable that much that happened should have happened. One naturally assumes that the greater the barrier the less chance of disseminules passing it and this is the general finding in phytogeographical studies. Two matters that have been little discussed but which have bearings on the subject of wide dispersal are the possibility of long-range transmission of pollen with the chances of introducing new genes by hybridization with taxa already established and the need to consider absentees from a flora when these might be expected on such hypotheses as continental drift.

However, there is no doubt that there have been great changes in the relationship of land and sea (often referred to as transgression or regression of the sea relative to the land), in the elevation and lowering of mountains, and in the origin and modification of deserts, even since the appearance of the angiosperms. It is not my purpose here to discuss the controversial subject of continental drift. I would only point out that for many phytogeographical problems the trangression or regression of seas *vis-à-vis* continental land is at least as important as any wandering of continents east or west or north or south. Shallow seas are as effective barriers to dispersal of land plants as are deep ocean basins of the same extent. A combination of studies of dispersal mechanisms with the reasonably established geological history of an area usually throws considerable light on the evolution of floras.

It is essential to emphasize the influence of man in the developmentof phytochoria. Man is the most powerful existing factor in modifying plant life, destructively and constructively, intentionally and unintentionally. Our attempts at nature conservation is an acknowledgment of this fact at the eleventh hour. Again, the subject is too great to deal with here even in general terms, but I would urge that the human factor in the evolution of floras always requires prominent treatment and often treatment separate from that devoted to other factors, though, of course, there must be final synthesis of the results of analysing factors separately.

Factors in the Evolution of Floras of the Balkan Peninsula.

Since most, though not all, of my examples are taken from the floras of the Balkan Peninsula a very brief outline of the geographical, geological, climatic, and human background is desirable. The Balkan Peninsula is the easternmost of the southern peninsulas of Europe and is separated from Asia Minor only by the narrow straits of the Bosporus, Sea of Marmara, and Dardenelles and by the broader but geologically recent Aegean Sea. The boundaries one gives to it are partly artificial especially in the north-west. Here they are accepted to include Istria and the Karst but to exclude areas north of the Danube and Save. In the east the Cyclades and northern Sporades are included but the Aegean Islands adjacent to the Anatolian coast are excluded. Crete is included but Karpatos is excluded. Geologically the Balkan Peninsula is both old and young. There is a central core, more or less triangular in shape and including the Rodope Massif, which has probably been land continuously from very early geological periods. Much of the present-day land surface around this old core is of Mesozoic or Cainozoic rocks with limestones, dolomites, and sandstones predominant. These strata have been much crumpled against the solid mass of old hard rocks, particularly in connection with the mountain-forming movements of Miocene times that gave rise to the Alpine folds. In Pliocene and Pleistocene times the geological history of phytogeographical importance has been largely connected with disruption. The formation of the Aegean Sea, for example, is of geologically recent occurrence. It has even been suggested that early man may have witnessed part of its formation by the foundering of faulted blocks. The old land mass, the surrounding folded mountains, the subsidence to the south and east, and the resulting increased erosion of many highland parts has led to the peculiar isolation of various parts of the Peninsula—an isolation reflected not only in floristic features but in human history from the Greek city states to the rise and frequent anatagonisms of the modern sovereign states.

Climatically, the Balkan Peninsula is included partly in the Mediterranean and partly in the Central European zones with transitional belts and many modifications associated with altitude and orientation. The area was, of course, affected by the Glacial Epoch, but, though the higher mountains in the north and centre were locally glaciated, there was no wide continuous ice sheet. It is, indeed, doubtful if there was much destructive modification of the flora as a whole at the peak of the Glacial Epoch but rather that there was enrichment by more northern elements immigrating into the existing flora. There was probably much more destruction with the on-coming of the cold in immediately pre-glacial times. The distinctions between the Mediterranean and Central European climatic zones are well known. The Mediterranean has hot dry summers with the main rainfall in the winter months which are relatively mild. In Central European climates the summers are warm the winters cold and the rainfall more or less distributed through the seasons. It follows that for plant life the most favourable periods for growth are in the Mediterranean zone the early summer and the autumn and in the Central European the summer. In the Mediterranean zone the summer drought is as much a limiting factor to growth as are the lower temperatures of winter.

The soils of the Balkan Peninsula are extremely varied. Owing to great erosion, whose rate has been greatly multiplied by the destructive influences of man, they are frequently shallow except in the plains and river valleys, but are often rich in food nutrients. Of particular interest are the wide occurrences of terra rossa, or red soil, of the karst limestones, soils derived from dolomitic rocks, and those from disintegration of serpentine.

The major biotic influence is undoubtedly that of man. Above all the destruction of forest and prevention of its rejuvenation have modified the flora and the vegetation. The climatic and edaphic conditions are favourable to the growth of high forest over most of the surface up to the altitudinal tree limits. The natural climax of forest differs from one area to another with climate and, to a less degree, other factors.

It is sometimes stated that the Mediterranean climate is not suited to tree growth but this is not true as a few now isolated and still decreasing forests, of, for example, *Pinus halepensis* Mill., show. There is also clear historical evidence of the former existence of forests in very many parts now bare of tree growth, both in Mediterranean and Central European climatic zones of the Peninsula.

The climatic, altitudinal, and biotic factors have combined to make marked altitudinal zonations of the flora and vegetation. In studying altitudinal zonation one has also to bear in mind the history of the flora from Tertiary times to the present.

Some Salient Facts in the Evolution of Phytochoria of the Balkan Peninsula.

We turn now to illustrate the evolution of floras by special reference to the Balkan Peninsula. A considerable amount of taxonomic and phytogeographical work has been done on the floras of this area in the last three decades, that is since I completed the text of my work *The Plant Life of the Balkan Peninsula* (Oxford, 1929). Much of the new research is included in the account of floral evolution that follows. We start with the Mediterranean areas. These include Crete, southern Greece, the Cyclades, the Adriatic coastal districts, and some parts of the northern Aegean coasts.

Crete is particularly interesting since it is the largest island within our geographical boundaries, and because of its position between the Balkan Peninsula, Anatolia, and North Africa, its wide range of habitats from the sea coast to the mountains with Mt. Ida 2457 m., and its relatively long isolation together with the internal isolation of four principal mountain groups. Over 1450 species are recorded from Crete of which about 150 are endemic to the island. Many of these last are very distinct and taxonomically isolated. Included are representatives of two endemic genera—*Petromarula* (Campanulaceae) and *Lyrolepis* (Compositae). One species of the genus *Ammanthus* (*Compositae*) has recently been found in the southern Cyclades, otherwise the genus is endemic in Crete. The endemics, on the whole, show taxonomic affinities with taxa that have more eastern ranges. The known connections between the floras of Crete and North Africa, particularly Cyrenaica, have been slightly increased by recent discoveries, both in Crete and in Cyrenaica. However, these connections are still insufficient to postulate an important and a geologically recent influence of the floras of these areas one on the other. More westerly past land links between southern Europe and North Africa, between Sicily and Tunis and between Spain and Morocco, are phytogeographically much more in evidence floristically. The relationships between the floras of Crete and Anatolia are strong and are confirmed by the recent studies of the floras of Karpatos and the Aegean area with its numerous islands. Crete is closely connected floristically with Greece. One may say that, in general, studies of the ranges of taxa agree with the geological and geographical findings that Crete is the outer edge of an Aegean continent now largely sunk beneath the sea. There can be no doubt that interchange of taxa occurred across this continent which disintegrated in geologically recent times. As interesting as lines of immigration are the study of relict taxa and *in situ* formation of taxa in Crete. An example of altitudinally vicarious species may be mentioned : *Chionodoxa cretica* Boiss. et Heldr. is known from Sphakia, Ida, and Lassithi, 1300–1700 m., and *C. nana* Boiss. et Heldr. from the same mountains at altitudes between 2000 and 2300 m. There is a record of *C. cretica* from Rhodes, but I have not been able to confirm this. As relict taxa we have *Petromarula pinnata* A.DC., whose nearest taxonomic relative is *Podanthum* an eastern Mediterranean genus, and *Lyrolepis* of the Carlineae tribe of Compositae only known from the island of Dia off northern Crete.

The Peloponnese and southern parts of continental Greece north of the Gulf of Corinth are within the Mediterranean Region, however this be defined. The topography which splits the surface into promontories, some islands, and mountain masses separated by plains or, at least, lower lying areas, has resulted in many isolated habitats which condition favours species formation as may also the great outcrop of limestones. The flora is consequently rich, with some 3000 species of which very nearly one-tenth are endemic. An analysis of the flora shows again that it has an old Mediterranean basis of " omni-Mediterranean " taxa largely added to by immigration from the east, a very considerable *in situ* evolution, and relatively few immigrants from the west and south and not many from the north. The *in situ* development is particularly well exemplified by a study of the mountain floras. Many of the species are endemic to Greece or at least to the Balkan Peninsula but time and again we find they are related to species of lower altitude occurring in the same geographical areas. There is much altitudinal vicarism. This is seen in such genera as *Astragalus, Allium, Silene, Salvia, Campanula, Achillea, Centaurea,* and many others.

The Cyclades are said to represent the unsubmerged remnants of a former Aegean continent. Floristically they are stepping stones between Greece and Anatolia. There are, however, many peculiar details in their floras. Attention may in particular be called to the fairly numerous species which " jump " the Cyclades. These are very often mountain plants and there is only one peak in the Cyclades over 1000 m. (in Naxos). It is also true that the Cyclades lack certain genera or subgenera that in other Aegean areas are rich in microspecies. There are about 36 endemic species known from the Cyclades but some of these need further collecting and examination. Very few are taxonomically isolated, though *Eryngium amorginum* K. H. Rechinger and *Centaurea oliverianum* DC. may be so classified. A good many are known from single islands, but this may be due to incomplete field work. A certain number of non-endemic species have the centre of their ranges in the Cyclades and may well have spread thence.

The extreme western margin of the Balkan Peninsula forms the eastern coast of the Adriatic Sea. A Mediterranean flora extends from western Greece northwards to southern Istria with gradual diminution in number of species and the development of some new endemic species. The general Mediterranean character of the coastal, lowland, and hill floras is certain though there is some mixture in places with species characteristic of other than true Mediterranean phytochoria and such become more abundant as one goes inland from the coast or northward along the coastal areas. The most interesting phytogeographical feature is the long steep Dalmatian coast with the numerous peninsulas and islands. These have been unequally studied botanically but one would have expected a greater number of endemics than the 25 to 30 so far recorded. The possible explanation is that the present insular isolation is geologically not very old so that few relicts of very limited ranges have been preserved and few neo-endemics have arisen.

The Aegean parts of Thessaly, South Macedonia, and Thrace, as well as the islands of the northern Aegean have a flora which is predominantly Mediterranean near the coast but is less typical than that farther south and only a short distance inland infiltration of more northern types is obvious. There is less endemism amongst the Mediterranean taxa and the mountain plants show more Tertiary relict or Central European affinities than in southern Greece. The influence of the Glacial (or Diluvial) Period is more marked on the flora as a whole than it is farther south. The Athos Peninsula is of very considerable phytogeographical interest. The peak (1935 m.) is of marble but much of the rest of the Peninsula has soils derived from non-calcareous rocks. The lower vegetation zones have a definite Mediterranean flora but the ridge has considerable extents of deciduous forest with *Castanea,* oaks, *Fagus orientalis* Lipsky and species of other genera. There are examples of inverted zonation due presumably to " frost pockets " with *Pinus halepensis* Mill. and *Erica* communities above deciduous woodland. About 20 species are now known in this small area that have not been found outside it. Some of these are taxonomically rather isolated, as *Helichrysum virgineum* Griseb. and *Silene orphanidis* Boiss., but others are more or less closely related to northern or southern species. A peninsula such as Athos shows a degree of isolation only slightly less than that of an island, and the fact that its flora and vegetation has been interfered with by man less than that of most parts of the Mediterranean Region, at least up to the last two decades, makes one wish it could be made an international botanical reserve, at the cost of one hydrogen bomb or one sputnik.

The areas in the Balkan Peninsula that, in general terms, are transitional between the true Mediterranean and definitely Central European phytochoria have their own botanical problems. There is a general tendency for the coastal and lowland floras to be more Mediterranean and the montane and high mountain floras to be more Central European. This is well seen in Thessaly, South Macedonia, and western Thrace and even in South Bulgaria. It is quite evident in these and other areas that one cannot usually draw a sharp line between the major phytochoria but only more or less broad transitional belts. There are many palaeoendemics especially in the mountains and these, on a variety of evidence, have to be largely accepted as Tertiary relicts. It is important to note that the Central European and, somewhat less, the transitional areas have mountain floras largely not immediately derived from the lowland floras and in this there is contrast with the Mediterranean floras. On the whole, the evidence is in favour of a northern and inland extension of the Mediterranean flora in post-glacial times. This is partly due to sight secular climatic changes and partly to the direct and indirect influence of man on the vegetation and flora.

The Thessalian Mt. Olympus (2918 m.) has many features of interest as bordering a transitional area. Its lower zones have a Mediterranean flora but above these the flora becomes transitional and is characterized also by 15 to 20 endemics, of which some are old or very old relicts. These last include *Ramonda* (*Jankaea*) *heldreichii* Benth. et Hk. f., *Brassicella nivalis* O. E. Schulz, *Achillea ambrosiaca* Boiss., *Centaurea transiens* Hal., *Campanula oreadum* Boiss. et Heldr., and *Verbascum malacotrichum* Boiss. et Heldr., while younger endemics include *Alyssum handelli* Hayek, *Cytisus demissus* Boiss., *Genista sakellariadis* Boiss. et Heldr., *Potentilla deorum* Boiss. et Heldr., *Peucedanum cnidioides* Boiss. et. Heldr., *Achillea olympica* (Heim.) Hal., and *Festuca olympica* Vetter. A number of old endemics extend from Olympus to a few other mountains. Thus, *Marrubium thessalum* Boiss. et Heldr., *Galium ossaeum* Hal., and *Allium heldreichii* Boiss. and also found on Mt. Ossa to the south.

The flora of Bulgaria is in the main Central European, but exceptions to this are the infiltrations of Mediterranean species and the older relicts and endemics. The steppe flora has also to be given separate consideration and the Pontic elements are important in the east. The Mediterranean infiltrations may be the most recent in the area and some are probably still extending their ranges. Of palaeoendemics there are many in the Rodope Massif, including *Haberlea rhodopensis* Friv., *Trachelium rumelicum* Hampe, *Scabiosa rhodopensis* Stoy. et Stef., *Geum rhodopeum* Stoy. et Stef., *Astragulus alopecuroides* L., *Sideritis scardica* Griseb., and many others. On the Rila are *Rheum rhaponticum* L., *Pinus peuce* Griseb., *Primula deorum* Vel., *Geum bulgaricum* Panč., and *Sedum tuberosum* Stef. On Ali Botuš occur *Viola delphinantha* Boiss., *Convolvulus nitidus* Boiss., *Rhamnus fallax* Boiss., *Fritillaria drenovskii* Degen et Stoy., and others. The Rodope Massif is, for the most part, a very ancient land mass and probably has been such continuously for at least long before the advent of the angiosperms. Along the Stara Planina are *Harberlea rhodopensis* Friv., *Prunus laurocerasus* L., *Daphne blagayana* Freyer, *Rhododendron kotschyi* Simonk., *Aesculus hippocastanum* L., and other ancient elements. Special mention must be made of *Astragalus physocalyx* Fisch. which is now apparently extinct in its only recorded locality near Philippopel. Numerous endemics which are best regarded as neoendemics are known for the Bulgarian flora especially in such genera as *Dianthus*, *Cytisus*, *Thymus*, *Centaurea*, *Hieracium*, *Achillea*, *Verbascum*, and *Viola*. The beautiful *Anthemis sancti-johannis* Stoy. Stef. et Turrill from the Rila probably comes into this category. Many of these "small" species may well be of post-glacial origin. Steppes in Bulgaria are largely of secondary origin following forest destruction by man. The steppe flora is heterogeneous. Much of it shows Mediterranean affinities but some species have immigrated from the east. The migration from south to north has occurred especially since the climate became warmer and drier in post-glacial times. On the

Black Sea coast there are a number of endemics of which *Lepidotrichum uechtritzianum* Vel. and *Colladonia triquetra* DC. may be mentioned. The low Strandja mountains in eastern Bulgaria and Thrace are particularly interesting. There is here a fine growth of forest recalling that of the northern parts of Asia Minor and the western Caucasus. This is marked by the presence of *Fagus orientalis* Lipsky, some oaks, *Rhododendron ponticum* L., *Daphne pontica* L., *Prunus laurocerasus* L., *Vaccinium arctostaphylos* L., *Epimedium pubigerum* Morr. et Decne., *Scilla bithynica* Boiss., and *Trachystemon orientale* D. Don.

It is convenient here to refer to several trees of special phytogeographical importance. The beech is widely spread in the mountains, especially in the " cloud-belt " zone of the northern and central parts of the Balkan Peninsula. The common beech of the Peninsula is certainly variable in characters of both vegetative and reproductive parts, especially in details of the leaves and cupules. It has been refered to by some authors as a subspecies or variety (*moesiaca*) of *Fagus sylvatica* L. or even named as a species. Up to the present there is incomplete comparative evidence to make this view acceptable. It leads to error to compare populations in one country with individuals in another and until full population studies are available over the whole range of *Fagus sylvatica* s.l. it is best to leave the microtaxonomy *sub judice*. Another factor complicating the taxonomy of the beech in the Balkan Peninsula is the occurrence over a much greater, though disjointed, range than was formerly known, of *Fagus orientalis* Lipsky. This species is now recorded from Thessaly, Athos, Thrace, Bulgaria, the Rodope Massif, and the Dobruja. Typically it is distinct from *F. sylvatica* in morphological characters and in ecology. However, there are many intermediates known, sometimes forming whole woods as above Aitos in the eastern part of the Stara Planina (Balkan Chain). These intermediates may be hybrids formed when the more northern common beech and the oriental beech extended their ranges and one introgressed into the other. The common beech is comparatively indifferent to soil conditions in the Balkan Peninsula and, so long as the substratum is well drained, it is found on silicate, limestone, igneous, and metamorphic rocks. Sometimes, however, it seems to avoid limestones nearer the southern parts of its range. Beech forests are, on the whole, better developed in the western than the eastern parts of the Peninsula. In some parts of Serbia and Bulgaria conifer woods are being superseded by beech woods.

The firs of the Balkan Peninsula are *Abies cephalonica* Link to the south, as typically in many of the mountains of Greece, and *A. alba* Mill. to the north with a broad intermediate belt of trees with mixed characters that have been lumped together as *A. borisii-regis* Mattf. and which seem relatively indifferent to the nature of the soil. Whether this last represents a kind of gigantic hybrid swarm or whether it is a relict population from which *Abies alba* separated out and spread north, even far into Central Europe, and *A. cephalonica* (often only on calcareous soils) separated out and spread southwards remains an open question. There are other, taxonomically closely related, firs in Anatolia.

Pinus peuce Griseb. is a beautiful tree endemic in Albania, North Macedonia, North Bulgaria, the Rodope Massif, Serbia, and Montenegro. It has five needle leaves on every dwarf shoot and is morphologically most nearly related to *Pinus wallichiana* A. B. Jackson (*P. excelsa* Wall.) of the western Himalaya. In the Balkan Peninsula it is a Tertiary relict. The same is true for the omorika spruce (*Picea omorika* Willk.) endemic in western Serbia, Montenegro, and Bosnia. This is the sole existing European representative of the section *Omorika*, whose other extant species occur in eastern Asia and North America.

Platanus orientalis L. is native in Crete (where an evergreen variant occurs), Greece, South Macedonia, Athos, Thrace, and the Rodope Massif. The other known extant species of the genus are natives of America and, one, of Indo-China. The oriental plane is a Tertiary relict in the flora of the Balkan Peninsula and must have been isolated geographically for a long period of geological time. Yet genetically it is not so isolated, since it has crossed with the American *Platanus occidentalis* L. to produce the London plane (*P.× acerifolia*) which is itself fertile, at least partially so, and produces offspring showing various intermediate or new characters.

Aesculus hippocastanum L. is known as a native of Greece, the Pindus, Epirus, and North Bulgaria. The other species of the genus are natives of eastern Asia and North America. The discontinuities in the present natural range of both the species and the genus accord with the accepted status of the horse chestnut as a Tertiary relict. The wide spreading of the tree as an alien in Britain and other countries and the biotypic variation it shows suggests that its present natural limitation in Europe is related to climatic changes within its original wider range and not to any deterioration within the species.

In the north-east of the Balkan Peninsula lies the Dobruja along the Black Sea up to the delta of the Danube. Here are the best developed steppes within the Peninsula, though, as in Bulgaria, many of them are secondary following the destruction of woodlands. The present steppe flora is in origin a mixture of species that have immigrated into the area from the south and east and some probably from the Hungarian steppes. In its sum-total composition it is of Recent origin since it mainly occupies loess covered land of Pliocene or Pleistocene dates. Again, one notes the number of Mediterranean species or of species closely related to those centred in the Mediterranean Region. Immigration is the key to the Bulgarian and Dobrujan steppe phytochoria. Above the steppe lands in the north there rise hills of older rocks with oak and more rarely beech woods. The older higher lands show a considerable number of old species including *Fagus orientalis* Lipsky, *Pyrus elaeagnifolia* Pall., and *Corylus colurna* L. *Sophora prodanii* G. Anderson may be of more recent origin. Other relicts of the Dobruja are *Goebelia alopecuroides* Burge, *Syringa vulgaris* L., and *Comandra elegans* Reichb. f.

The interesting ash *Fraxinus pallisae* Wilmott is more widespread than was known when it was first described from the Danube delta. It occurs also in eastern Bulgaria, in the Mesta delta area in western Thrace, and near the Danube in eastern Serbia. With *Fraxinus oxycarpa* Willd. it hybridizes to form hybrid swarms. That it has originated polytopically from this species is a possibility. Recently it has flowered and fruited at Kew from trees grown from Thracian seed.

The vegetation and flora of Yugoslavia, excluding the Adriatic coastlands, are essentially Central European but there is considerable evidence of infiltration of Mediterranean species into North Macedonia and Hercegovina and even much farther north. Serbia proper is the most inland of the areas of the Balkan Peninsula. The winter is often severe and in the early spring of 1956 a great many plants had been killed at Beograd, including the common box. Though the flora of Serbia includes 180 Balkan Peninsular endemics there are only about 7 limited to Serbia proper. The much smaller area of Montenegro has about 20 endemic species, Bosnia 22, and Hercegovina 11. The southern part of Hercegovina has to be relegated to the Mediterranean Region on the basis of its flora. South Croatia has 7 species known only from the area and Istria 7.

Albania has been practically closed to western botanists since the end of the second world war. Its flora is extermely interesting and includes about 320 species endemic to the Balkan Peninsula and about 50 known only from Albania. Its mountains, together with those near its borders but politically in Yugoslavia or Greece, have been a refuge for many relicts, including *Pinus peuce* Griseb. *Dioscorea balcanica* Košanin, *Forsythia europaea*, Deg. et Bald., *Wulfenia baldaccii* Deg., and *Ramonda serbica* Panč. North-eastern Albania and the nearby parts of North Macedonia, Novi-Pazar, and Montenegro are particularly rich in relict species. There is some justification for saying that the mountain flora is conservative. The southern extension of the Alpine flora (in the true geographical sense of species with ranges centred in the Alps of Central Europe and not " alpine " in the sense of merely occurring at high altitudes) in the western parts of the Balkan Peninsula has contributed an important element to the flora. There is a general reduction in the number of Alpine species from north to south as shown by the following figures : South Croatia 146, Bosnia 171, Hercegovina 127, Montenegro 173, Albania 108, Epirus 28, Greece 24, Crete 1. There is a marked break in the numbers of Alpine species somewhere in Albania, probably in a belt near the centre.

In the western parts of the Balkan Peninsula are the typical karstlands on limestones. These have certain well-known physiographic features such as little surface water, underground rivers, permeable terrain, great exposure of bare rocks, dolines, poljes, terra rossa soil, and so on, but there is more variation both locally and from one district to another than is often recognized. The limestones are mostly of Mezozoic and Cainozoic ages and thus differ from the limestone pavements etc. of western Yorkshire and other Carboniferous outcrops of northern England. Though great areas of karst are now devoid of trees, botanical observations and historical records both lead to the conclusion that this is a man-made feature. If man and his domesticated animals were eliminated the greater part of the karstlands would revert to forests, especially of oaks, though it might well take several centuries. The brushwood and ground floras are rich even when the vegetation is degraded. There is a considerable Mediterranean element with few true woodland plants that are not limited to still wooded localities. Karst phenomena are found in areas ouside the western Balkan Peninsula (from Istria and South Croatia to Montenegro) where they are best developed. Where limestones outcrop and are denuded of forest " karsting " commences when climatic conditions allow and increases when grazing and exploitation for firewood continues. Nowhere is the destructive and retarding influence of man on the flora and vegetation more striking than in the karst areas of Istria, Hercegovina, and Montenegro.

In the western parts of the Balkan Peninsula there are also considerable outcrops of dolomite and serpentine rocks. These give soils with a selective influence on the flora and a number of taxa are limited to them.

The probable history of the flora of the Balkan Peninsula has to be pieced together mainly from taxonomic, range, and distributional data and these interpreted in conformity with what is known of the geology and palaeometeorology. Direct and satisfactory evidence derived from fossil plants is still meagre. Some Tertiary deposits with plant remains have been described and we may note several of which accounts have been fairly recently published. In the Struma valley, beds dated as Miocene contained remains determined as belonging to the genera *Sequoia*, *Glyptostrobus*, *Taxodium*, *Carya*, *Betula*, *Ulmus*, *Salix*, *Populus*, *Quercus*, *Cinnamomum*, *Parrotia*, *Acer*, *Porana*, *Terminalia*, *Fraxinus*, *Myrica*, *Zelkova*, *Cassia*, *Fagus*, etc. Pliocene strata rich in fossil plants have been studied in the plain of Sofia by Stefanoff and his colleagues. The conclusions reached are of phytogeographical interest. The climate was less continental and more oceanic than it is now. Especially there was more abundant summer rainfall and greater humidity. There has been considerable reduction in the number of conifer genera in the area. The general result, presumably linked with the Glacial or Diluvial Period, has been a reduction in the number of common species in what were mixed forests, by extinction within the area or relegation to a relict nature of others, so that forests are now dominated by one or a few species. The fossil flora can, from this standpoint, be classified into several groups : (1) many species that are still common in Bulgaria or neighbouring areas ; (2) species still known in Bulgaria but which are now much restricted in range in this country, as *Prunus laurocerasus* L. and *Rhododendron ponticum* L.; (3) Mediterranean species whose northern limit of range is now farther south, as *Quercus ilex* L., *Q. coccifera* L., *Olea europaea* L., *Arbutus andrachne* L., and *Laurus nobilis* L.; (4) species of genera now extinct in the Balkan Peninsula, as *Tsuga*, *Cedrus*, *Pterocarya*, *Pasania*, *Sassafras*, and *Bumelia*. One may wonder if the biotype constitution of the recorded Mediterranean species may not have been different from what it is now if the summers were wetter. Such biotype change is suggested by the statement that the fossils of evergreen oaks show that *Quercus ilex* L., *Q. coccifera* L., and *Q. suber* L. segregated from a very polymorphic complex with evergreen habit.

Bogs are rare in the Balkan Peninsula and are, with few if any exceptions, found only in montane and high mountain areas. Two recent accounts of pollen analysis have some conclusions of phytogeographical importance. In Serbia, near Vranje, is the Vlasina moor in a depression at 1200 m. From borings, Černjaski recognised, from below upwards, a pine phase which, with increase in temperature, led to an oak phase, followed by a fir-spruce phase with increase in moisture, to the existing mixed beech-pine-fir phase of the montane climate. He concluded that the oak (oak mixed forest) phase of Vlasina is older than the beginning of the Atlantic phase in Central Europe. In the Vitoša near Sofia, Bulgaria there are, in the higher parts, numerous small bog deposits. Stoyanoff & Georgieff sampled eleven of these between 1680 and 2200 m. The bogs were not all of equal size, depth, or exactly similar age. In the lower layers were found very considerable amounts of *Abies* pollen a genus that is now rare on Vitoša. Pine pollen, probably from *Pinus peuce* Griseb., was also abundant, though only a few individuals and isolated groups of this Tertiary relict are now to be found on Vitoša. Beech pollen tended to increase in the upper layers. This is in conformity with other evidence from the mountains of Bulgaria and neighbouring lands that in more recent times beech has replaced conifers. Other pollen found was of elements that are still present on Vitoša and it is concluded that there has been little qualitative but some quantitative change since the peat was formed. Comparison with the pollen analyses described for other countries suggest that the peat formation began in Subatlantic times.

The general evidence is that the Glacial Epoch and specially its oncoming resulted in a twofold change in the flora of the Balkan Peninsula : first, in the central and northern parts there was such increase in severity of the climate that many species and genera were exterminated and many others were reduced to relict status, and secondly what had been more northern elements were "driven" southwards and found refuge in the Balkan Peninsula where they now occur mostly in the mountains. During and since the Glacial Epoch there have been climatic fluctuations. Mediterranean elements had their northern ranges pushed southwards and later, with the development of warmer and drier conditions, again extended northwards by infiltration.

The influence of man on the vegetation and flora of the Balkan Peninsula has been very great. The Mediterranean Region is the cradle of modern western civilisation and from Minoan and Mycenean times onwards, if not earlier, forests have been destroyed and often prevented from rejuvenating, marshes have been drained, flocks and herds have been pastured from the lowlands to the uplands, new habitats have been created allowing spread of ranges to species able to colonize them, species hitherto geographically isolated have intermingled and sometimes hybridized, in many ways alien species have been introduced and some have established themselves even to become rivals to the native plants.

Concluding Remarks.

In illustrating the evolution of floras in the Balkan Peninsula it is obvious that only some of the major problems of phytogeography are included and that there are considerable limitations due to incomplete knowledge in dealing even with these. Questions concerning floristic connections across what are now great ocean basins and the possibilities of sunken continents or continental drift have only remote relevance. It has to be noted, however, that there are as many, and as difficult, problems connected with disconitnuities of range of taxa over what are at present continuous continental surfaces as with discontinuities across the Atlantic, Pacific, Indian, or Antarctic (or Subantarctic) Oceans. Taxonomists can give numerous examples of such, though some phytogeographers appear to ignore them. While much is known about the geological hstory of the Balkan Peninsula there is relatively little reliable palaeobotanical knowledge available concerning this area. Much remains to be done concerning the existing flora. Intensive collecting, especially in parts of Greece (in the sense of the modern kingdom), Thrace, Albania, and parts of Yugoslavia, is needed. Various genera require monographing by modern methods. Little is known regarding the cytogenetics of Balkan Peninsular plants from material of direct wild origin and it is obvious that there is a wide field of research here because of the large number of old and new endemics in many of the phytochoria.

Enough is known, however, to make the following generalizations reasonably certain regarding the floras of the Balkan Peninsula and some, at least, of these generalizations hold for other areas of the world :

1. In origin and development floras are generally complex. This is true for major phytochoria, such as the Mediterranean and Central European Regions, and for subdivisions within these. A " flora " is nearly always a mixture, not merely of taxa but of taxa of different phytogeographical origins, of different histories, and because of habitat diversity within an area, of different ecologies.

2. *In situ* development, by mutation, hybridization, and segregation, gain by immigration of taxa and biotypes new to the area, and loss by emigration or dying out, have all occurred.

3. Present ranges can frequently be correlated with existing climatic, edaphic, and biotic factors but it is clear that such ranges are only relatively stable.

4. The ranges of many taxa have had a variable history that can sometimes be correlated more or less closely with known facts of the geology of the area, but some remain puzzling. Intensive autecological studies, observational in the field and experimental, combined with cytogenetical research might throw much light on some of these.

5. There are numerous difficulties and risks of error in the synthetic approach to taxonomy and phytogeography and many conclusions must remain tentative. In synthesis we meet especially the dangers of speculation. There is always the need to keep facts and hypotheses distinct, and to remember that the former are always incomplete as soon as they cease to be isolated while the latter are always liable to alteration. On the other hand, the advantages of attempting to link up the different approaches to one main subject are very great. Light is often thrown on what at first seem to be isolated problems. Thus, a phytogeographical classification often elucidates taxonomic difficulties while reciprocally a new taxonomic classification may solve a phytogeographical problem. The synthetic method at least avoids the reproach of extreme analysis that one merely learns more and more about less and less.

EXPERIMENTAL APPROACHES TO THE PROBLEMS OF GROWTH AND FORM IN PLANTS

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Methods in plant morphogenesis. By C. W. Wardlaw, Department of Botany, University of Manchester

1. INTRODUCTION

The term *morphogenesis* connotes the genesis or origin of form—or, in the words of the *Oxford English Dictionary*, 'the origination of morphological characters'—and, by extension, the related structural details. Both parts of the word are therefore of high significance: together they convey, to the biologist, the idea of the coming into being of visible and tangible shapes or patterns, as in the growth of an organism from a fertilized egg to the full manifestation of its distinctive characters in the adult state. Morphogenesis is a comprehensive subject, admitting of many approaches and therefore of many investigational techniques. Indeed, if we hold that the eventual aim in morphogenesis is to give as full an account as possible of the progressive manifestation, or expression, of the distinctive characters of organisms during their development from the zygote onwards, it is well nigh impossible to say where the study of morphogenesis begins and where it ends. In practice, however, and with some necessary reservations, science tends to advance more rapidly when individual projects are clearly defined and separated off for special study. My task this morning is to indicate some of the methods which have have enlarged our understanding of morphogenesis.

In general terms, one might say of the several disciplines that contribute to morphogenesis that:

(i) morphology is concerned with the visible evidence of formal and structural developments in embryonic, growing and maturing regions;

(ii) physiology is concerned with the phenomena of metabolism and growth; in particular with the identification of the specific substances involved, and with the patterns of distribution of those metabolites which precede and determine the earliest visible developments;

(iii) the specific nature and characteristic sequence of metabolic patterns during ontogenesis are, directly or indirectly, determined by elements in the genetical constitution;

(iv) all morphogenetic processes have physical and mathematical aspects of the kind expounded by D'Arcy Thompson.

Some progress has been made along each of the lines indicated above. Nevertheless, it is important to recognize that the results of individual analytical or experimental investigations do not, in themselves, enable us to explain the inception of form, i.e. how the many processes involved are so timed and integrated that a living entity, exemplifying developmental harmony, comes into being; how specific and distinctive organization, and seemingly appropriate functional activities are evident at every stage; in short, how an individual of a particular species, recognizable 'by head', results. Thus although we are specially concerned with experimental investigations in this symposium, it seems to me that approaches other than experimental ones are both valid and desirable in this introductory paper.

2. MORPHOLOGICAL OBSERVATIONS

Although we have a very considerable fund of information on the form, structure and histology of plants, including their embryology, there is still need for further work. This point deserves some emphasis; for there can be no true understanding of morphogenesis unless there is precise observation of the size, shape and relationships in time and space, of nascent organs in embryonic regions. This work is often considerably more difficult to carry out than is sometimes thought; and, accordingly, it is sometimes neglected or insufficiently well done. But without this exact preliminary information, there can be no proper formulation of the relevant physiological problems nor can an adequate experimental or analytical programme be designed. If, for example, the relationship of a very young leaf primordium to the apical meristem is inaccurately observed, the interpretation of certain experimental observations is likely to be less sound, or less accurate, than it might be. There are also experiments in which it is important to know whether a young leaf primordium is in early or in late plastochrone. The basic method, indeed the *sine qua non*, in morphogenesis, therefore, is the precise observation of embryonic regions. These are usually small, delicate, and sometimes rather inaccessible; but they must be brought under direct observation and kept alive if an experimental programme is to be carried out.

3. SURGICAL TREATMENTS AND THE RELATIONSHIPS OF ORGANS AND TISSUES

Among the most distinctive features of plants are their size and shape, and the relationships in space of the component organs: thus shoots may be long or short, simple or much branched; leaves may be small or large, simple or compound, and variously disposed on the stem; and comparable remarks could be made of flowers and inflorescences. There may also be more or less conspicuous morphological changes during ontogenesis, e.g. heteroblastic development, or the transition from the vegetative to the reproductive phase. In each instance, the primary pattern of development, i.e. the primary shape and relationships of organs, and the pattern of their tissue systems, is determined at an apical meristem. As these morphogenetic activities usually take place with considerable regularity, the growth of the plant from the zygote to the adult state exemplifies what Thoday (1939) has aptly described as developmental harmony. These simple observations invoke a host of fundamental questions. They have often been stated and need not be repeated here (see Wardlaw, 1952). But if, for example, our aim is to investigate factors which may determine the inception, growth, and form of particular organs, their mutual relationships, regulated development and the differentiation of their tissues, what experimental procedures are available? In general, the experimental method requires the separation of organs one from another, e.g. of a leaf primordium from the apical meristem or from adjacent primordia, followed by observation of the nature and course of development in the new situation thus created. In this connexion the use of surgical techniques has proved to be of considerable value. Although this approach to the investigation of embryonic tissues has its disadvantages and limitations, and is, indeed, open to various objections, nevertheless, it is a simple fact that surgical procedures have yielded information which, to date, has not been forthcoming from any other experimental procedure. Here reference may be made to the experimental investigations of phyllotaxis by M. & R. Snow (1947), and of the various organogenic and histogenic activities of the shoot apex by Ball, Wetmore, Sussex, Cusick, Cutter, Steeves, Wardlaw and others. In parenthesis, I have long been aware of the limitations of this approach: there must, it would seem, be a limit to the number of ways in which the shoot apex, leaf primordia, etc., can be incised with useful results. It is surprising, however, how many instructive experiments can be based on surgical techniques, the more so when one bears in mind the possibility of combining these with localized chemical or more general nutritional treatments. Here I would call your attention to the very interesting experiments of Camus (1943–5) and of Wetmore and Sorokin (1955) on the induction of vascular tissue in undifferentiated tissue-culture callus by grafting in young buds, with and without applications of auxin, and indeed, by the application of auxin alone to the graft incision. Gregory & Veale (1957) have shown that the classical experiment of removing the shoot apex to induce or promote the development of lateral buds, can be made to yield yet further information by simultaneous auxin or nutrient treatments. There are also the recent studies of regeneration of vascular tissues after incision by Jacobs (1952) and Jacobs & Morrow (1957)—work pioneered by Simon in 1908—in which he has demonstrated a close quantitative relationship between the downward movement of auxin and xylem differentiation. Surgical techniques have also been used, with good results, in the investigation of roots and of the gametophytes and young embryos in hepatics and ferns.

4. Developmental physiology

The physiology of development covers a vast field of which only the most general indications can be given here.

Biochemical investigations. Since all morphogenesis involves metabolism, there is virtually no limit to the relevant biochemical problems; and similarly, other branches of plant physiology are more or less directly involved. This is necessarily so, since, at base, all morphological development results from the functioning of genetically determined reaction systems in particular environments. What is commonly described as Developmental Physiology is the subject of a considerable book by Bünning (1948) and has many contemporary adherents.

From the time of Sachs, who laid the foundations of biochemical morphogenesis in plants, attempts have been made to discover the nature and functional significance of the substances, both general and specific, that are present in embryos and in the apical growing points of shoots, leaves, roots and flowers. Considerations of time and space do not admit of reference being made to the many valuable chemical analyses of embryos and apices in which the presence of carbohydrates, amino acids, auxins, enzymes, etc., have been reported. Reference might here be made to the work of Steward and of R. Brown and their collaborators. It is, of course, evident that this kind of information is essential to a more adequate understanding of apical growth and morphogenetic activity, though, in the present stage of knowledge, only some of it has an immediate application. One direct use of the new information in morphogenetic investigations, namely the improvement of tissue and organ culture media, may be mentioned (Wetmore, 1953, 1954, 1957).

Tissue culture. Although this is now the subject of a vast literature, only a relatively small part of it has so far shed any direct light on morphogenetic processes. The most interesting and illuminating discoveries include those in which the formation of either roots or buds has been induced by the addition to the standard medium of certain substances, e.g. adenine and indole-3-acetic acid (IAA), in particular concentrations (Skoog, 1954; Skoog & Miller, 1957; Skoog & Tsui, 1948). The aseptic culture of single cells, or of small groups of cells, in media of known composition, and their further growth into organized structures, which has now been achieved, is not only a realization of Haberlandt's classical concept of tissue culture, but opens up fascinating and important fields for further exploration (Steward, Mapes & Smith, 1958). It has also been shown by several investigators, Rijven (1952, 1956), Haccius (1955), Rietsema, Satina & Blakeslee (1953–4), Rietsema, Blondel, Satina & Blakeslee (1955), Tukey (1938), and others, that the normal course of embryonic development can be modified by excising young embryos and growing them under controlled conditions, or by treating them with physiologically active solutions while they are still in the seed. The growth and further development in pure culture of young fern sporophytes, excised fern and other apices, young leaf primordia, roots, immature fruits, and ovules, as reported by various investigators, open up virtually inexhaustible fields for new work on morphogenesis (refs. in Steward *et al.* 1958).

Before leaving this topic I ought to mention the very interesting investigations by Wetmore & Morel (1951) and Freeburg & Wetmore (1957) on the pure culture of gametophytes of *Lycopodium* spp., and by Allsopp & Mitra (1958) on the pure culture of mosses.

Direct and indirect chemical treatments. Because of the minute size and inaccessibility of the embryo or the shoot apex, many experiments on chemical morphogenesis consist in applying growth-regulating substances to the soil or to leaves of different ages, in the hope, or expectation, that some of the substance applied will be translocated to the shoot apex and there induce morphogenetic effects of a novel kind. Such experiments are now the subject of a very considerable literature in which many anomalous developments, usually in the adult stems, leaves, flowers, etc., have been illustrated. This experimental approach has shown that many specific substances, both natural and synthetic, disturb the normal metabolism and morphogenetic activity of embryonic regions; but the work would undoubtedly gain in value if the earliest changes effected in the apex were more closely observed. Many physiologically active substances have also been incorporated in tissue-culture media, but to date, this procedure has added rather less to our knowledge of morphogenetic processes than had perhaps been expected.

It may be that the specific substance, though present in the medium, does not reach those regions of the tissue culture, e.g. its upper surface, which are capable of morphogenetic activity. Wetmore (1953, 1954), for example, found that excised apices of *Adiantum pedatum* L. could be induced to grow more slowly or more rapidly by changing the composition of the culture medium; but none of the specific substances tested altered the fundamental morphogenetic pattern of the apical meristem. Contemplation of this fact led me to observe the action of various physiologically active substances when they were applied directly to apices of '*Dryopteris aristata*' (*D. dilatata* (Hoffm.) A. Gray) which had been laid bare by the removal of all older primordia and scales. In fact when substances such as IAA, IAN, vitamin B, etc., were applied in this manner, the normal organization and morphogenetic activity of the apical meristem were more or less considerably modified. In different instances, the more conspicuous results included the inception of double leaf primordia, the formation of buds in leaf sites, the development of a sunken meristem by the upgrowth of the subapical region, the cessation of primordium formation, and the parenchymatization of the meristem, culminating in the outgrowth of scales from the former site of the apical cell (Wardlaw, 1957 *a*). In short, several of the characteristic modifications obtained by surgical techniques resulted from these direct chemical treatments. Along the same general lines, interesting observations have been recorded by M. & R. Snow (1937); Ball (1948); Gorter (1951) and Wardlaw & Mitra (1958); and by Rietsema *et al.*, Haccius, and others, on young embryos. Of course, it is one thing to induce these interesting morphogenetic developments: it is a task of considerably greater magnitude and difficulty to explain them. These observations all relate to the vegetative apex, but chemical treatments applied to plants at the onset of flowering, as demonstrated by J. & Y. Heslop-Harrison (1957 *a*, *b*) and others, have also yielded results of very considerable interest. It need hardly be said that there is virtually unlimited scope for further work on experimental morphogenesis in the rich assemblage of materials afforded by the flowering plants.

The genetical approach

An extensive literature testifies to the fact that the distinctive form and structure of the individual organism are fundamentally determined by its genetical constitution, though factors in the environment are always at work and may also have more or less conspicuous effects. This general statement introduces a vast and complex subject; for although all the elements of the genetical constitution are present in the zygote, different genes, or groups of genes, may differ greatly in their time of action and in the magnitudes of their effects. Contemporary investigators of physiological-genetics and of morphogenesis are concerned with such searching questions as: in embryonic regions, how and when do particular genes and their products, reacting in the cytoplasm, determine, or contribute to, the primary morphogenetic pattern and its subsequent amplifications? This kind of inquiry is obviously complex and difficult, but at least a beginning can be made by close comparative observations on the growth, morphology, anatomy and histology of primary embryonic regions, e.g. shoot apices, in related materials which have been studied genetically; and, better still, where characteristic differences in metabolism and/or growth can be referred to particular genes. In shoot apices of diploid and tetraploid *Vinca rosea*, the distal embryonic cells of the tetraploid have the same anticlinal dimensions as the diploid, but 1·5 times the periclinal dimension. Differences in the size and cellular constitution of the shoot apex in diploid and tetraploid maize, and some consequential growth and morphogenetic differences, have also been reported. The periclinal chimeras in *Datura*, described by Blakeslee and his colleagues, are too well known to need special mention here (see Wardlaw, 1957*b*, for refs.). Morphogenetic studies of the shoot apex and its primordia in *Nymphaea* and *Nuphar* by Cutter (1957) have shown that certain relationships, important in taxonomy, are evident during early organogenesis but would almost certainly escape observation during the later development. Different genetical effects in early organogenesis are well illustrated by studies of leaf formation; for whereas many leaf primordia are very much alike at their inception on the apical meristem, specific and distinctive differences can already be observed in the subapical region. In some species, the base of the primordium remains small and discrete, whereas in others it extends round the axis to form a sheathing organ as in the Umbelliferae and many monocotyledons. The evidence to date is that differences in the genetical constitutions of related species and varieties may be reflected in the size of the embryonic cells and in the differential or allometric growth pattern. The diversity in floral structure, indicated in taxonomy by contrasted terms such as polypetaly and gamopetaly, hypogyny and epigyny, apocarpy and syncarpy, etc., can all be referred to differential growth during floral organogenesis. How genes determine the pattern of growth, and how mutant genes may modify that pattern, are complex problems, but we can, I think, see how a beginning can be made.

The effects of ionizing radiations and of mutagenic substances would be included under the general heading of this section (Gunckel, 1957; Gunckel & Sparrow, 1954; Sparrow, Gunckel, Schairer & Hagen, 1956).

Mathematical analyses

In all but the simplest organisms, the ontogenetic development, from the zygote to the adult state, is characterized by changes in size, form and structure. Roots apart, all the primary developments in vascular plants can be referred to the activity of the shoot apical meristem. These developments usually take place with very considerable regularity and fidelity. In some species the successive and characteristic changes in form during ontogenesis have been related to the nutritional status of the apex and analysed in terms of the distribution of growth. According to thinkers such as D'Arcy Thompson, the whole of this regular morphogenetic development lends itself to mathematical treatment; and more recently, investigators such as Schuepp (1952), Abbé & Stein (1954) and Richards (1948, 1951) have shown how much new light may be shed on the growth, morphogenetic activities and regulated development of the apex by a percipient mathematical approach.

Applied morphogenesis

It is probable that morphogenesis is generally regarded as a somewhat academic study. Yet a little reflexion will show that it has, or could have, an important applied side. Many horticultural practices, such as pruning, fertilizing at particular times, vernalization, photoperiodic treatments, the production of seedless fruits, the prevention of fruit and leaf fall, etc., are fundamentally concerned with morphogenetic processes. Time does not admit of more than this passing mention of the possibilities of a still wider application of a knowledge of morphogenesis to agriculture and horticulture.

Organization

Whatever the species, the orderly ontogenetic process culminates in an individual of characteristic size, shape and distinctive appearance. In its organization, which we may define as the summation of its genetical constitution and its specific, orderly development, one species usually differs in certain relatively minor characters from a closely related species, and more or less considerably from a distantly related species. There is, however, the familiar but remarkable fact that closely comparable, major organizational features are present in organisms which, on taxonomic grounds, are quite unrelated. All vascular plants, for example, are characterized by an axis surmounted by an apical meristem which gives rise to the lateral members, leaves, buds, etc., in a regular manner. The same pattern of phyllotaxis may be observed in ferns and higher plants. Solenostelic vascular systems are known in *Selaginella*, ferns and flowering plants; heterospory has evolved independently in unrelated groups; and so on. These close similarities of development, whether in related or unrelated species, have been described as *homologies of organization*, and it has long been recognized that they are widespread in the Plant Kingdom. So we have to account for the fact that organisms in different lines of descent, and presumably with quite different genetical constitutions, may have major organizational features in common. This is not only a phenomenon of great interest in evolutionary biology: it is clearly of great importance in causal investigations of form and structure. Some botanists may perhaps regard notions such as those of organization and of holism—the concept that organisms develop as integrated wholes—as being self-evident truths and beyond the reach of practical investigation. Nevertheless, they are fundamental phenomona and some attempt to understand how the specific organization of individual species, and how homologies of organization are determined, is of the very essence of biological inquiry. Since homologies of organization have a real existence, it seems probable that common factors determining systems of a general kind may be involved. In this connexion the diffusion reaction theory of morphogenesis advanced by Turing (1952) may be mentioned as being of the kind that is of special interest. Among other points, he indicated that comparable patterns may be produced by reaction systems of quite different constitution. The validation of this, or indeed of any other similar theory which rests on a physico-chemical basis, will depend on evidence of its generality and on experiments in which the reaction system can be disturbed in characteristic ways with predictable results.

The results of the normal morphogenetic activities in any species, beginning with the zygote, are seen in the appearance of its taxonomic characters, and in the progressive manifestation of its specific organization and holistic nature during ontogenesis. To this fascinating and endlessly diversified field of inquiry there are clearly many approaches.

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Effects of the environment on leaf development in Impatiens parviflora DC.

By A. P. Hughes, Botany School, University of Cambridge

(With Text-figures 1–5)

A good deal of quantitative information is already available on the growth of *Impatiens parviflora* DC., a species belonging to the small class of annual plants which form natural communities in a range of light conditions from full daylight to dense shade. This short paper on leaf development deals with only part of the more general problem of the autecology of a shade plant and describes one aspect of the effects of the aerial environment on the growth and form of this plant.

It has been found that the distribution of dry weight between the leaves and the rest of the plant has the same relationship irrespective of light intensity, or of temperature and humidity in the range so far studied. However, for a given total dry weight, say 150 mg., the leaf area may range from 20 to 80 cm^2 from full daylight to dense shade. This indicates that the differences in leafiness are principally due to differences in the spatial distribution of the same amount of dry matter. The very wide range of leaf structure found under various levels of shading, in association with other marked modifications of form, make *I. parviflora* a most suitable subject for a study of the factors affecting leaf development. It is surprising how little information is available from botanical and agricultural literature on a subject so fundamental to plant growth as the basic understanding of leaf morphogenesis. Such information as may be found describes isolated

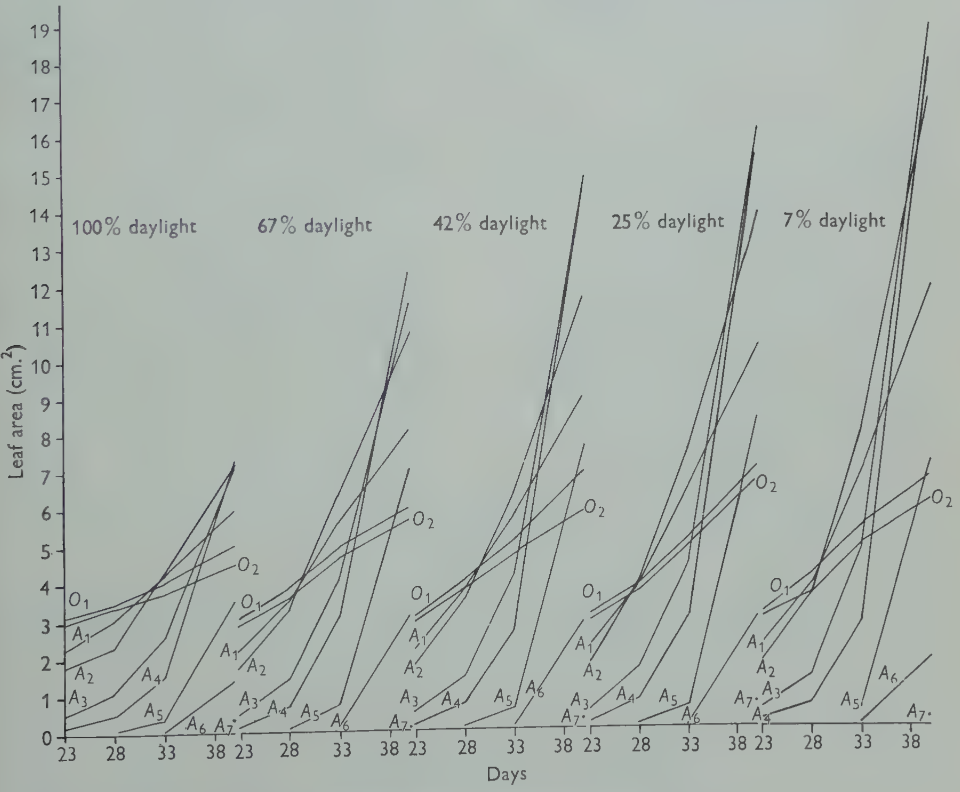

Fig. 1. Growth in area of individual leaves at various levels of shading. O_1, O_2: opposite leaves; A_1, etc.: alternate leaves.

pieces of experimental work, mainly on mature tissues and with little reference to physiological performance. However, the functional behaviour of the leaf forms described here does not lie within the immediate interest of this Symposium.

The full scope of these investigations has included experiments out of doors, both in the open and under screens transmitting various fractions of daylight from 100 to 7 %, and indoors in cabinets giving full control of the aerial environment. The illustrations for this paper are drawn from plants grown out of doors, but experiments in the cabinets show that a similar pattern of growth occurs there.

Plants were grown in pots and transferred to the various screens when the cotyledons had emerged. Healthy growth took place in all sites, but the heaviest and tallest plants were found in the middle of the light range (67, 42 and 25 % daylight). The plants in full daylight were shorter, sturdier and showed slight epinasty of the leaves. Those in 7 % daylight were also shorter, but the more obvious features were the delicate stems and leaves. Lateral branches developed in the axils of the cotyledons and first two leaves in all but the 7 % plants.

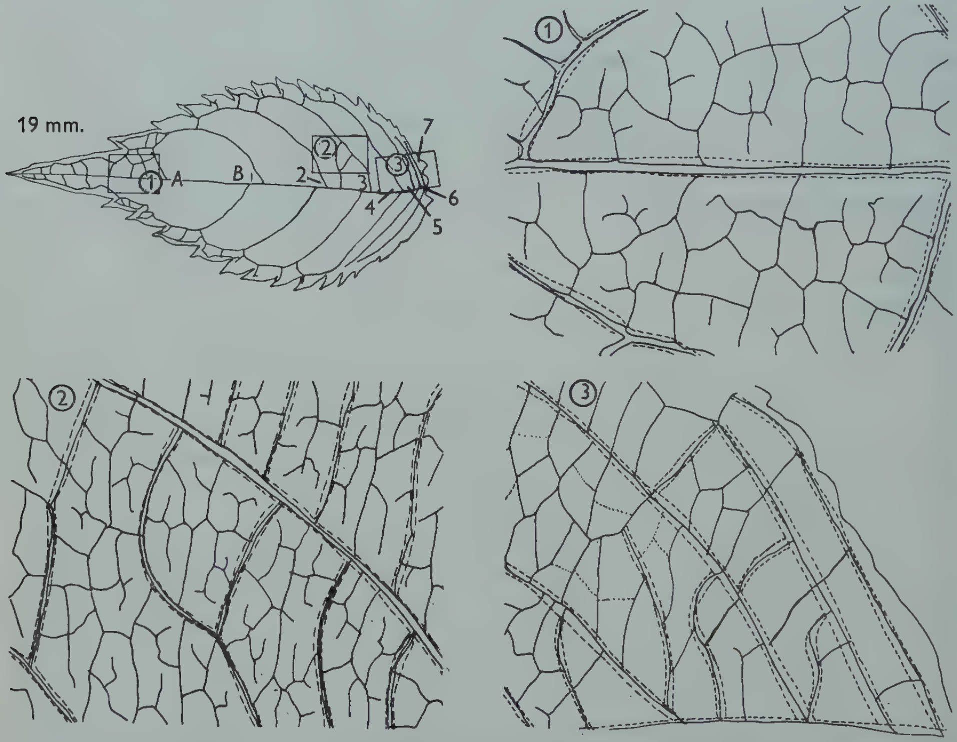

Fig. 2. Development of leaf venation. Dotted lines indicate procambial strands, broken lines show veins with bundle sheaths. Approximate magnification: leaf, × 3; regions 1–3, × 240.

The leaf area must be considered next in terms of the number and size of the individual leaves which compose it. Fig. 1 shows the growth curves for growth in area of the leaves on the main axis in the various conditions. Two effects are obvious (*a*) that leaves at the same insertion are progressively larger with decreasing light, and (*b*) that successive leaves on any one plant are larger. This discussion will be confined to the ecological effect, leaving the heteroblastic phenomenon for another occasion. In consequence the general pattern of leaf development applicable to all leaves will be described next, and then a comparison of the structure of leaves from full daylight and 7 % daylight will be made. The other light conditions provide intermediates between these extremes.

The venation and internal anatomy have been investigated by clearing whole leaves and by sectioning in transverse and paradermal planes. Fig. 2 shows the appearance of a half expanded leaf. At the base (region 3), veins of the second order (B series) are found, with only a few tertiary cross-veins. Nearer the apex is a zone where quaternary and quinary veins block out a continuous closed matrix. Procambial strands and various stages of their differentiation can be clearly recognized and are shown as dotted lines in the top left of Figs. 2, 3. As vacuolation and expansion occur (region 2), disruption of the single files of tracheids in the veinlets of the ultimate order occurs, giving rise to blind vein endings (Slade, 1957). The rupture is usually at the junction between veinlets and, with few exceptions, is in single tracheid veinlets only. At the apex (region 1) the fully mature lamina is found. This sequence in space represents the series in time at any one place. The type of leaf development is therefore basiplastic with a ground mesophyll which segments procambial strands of higher order successively.

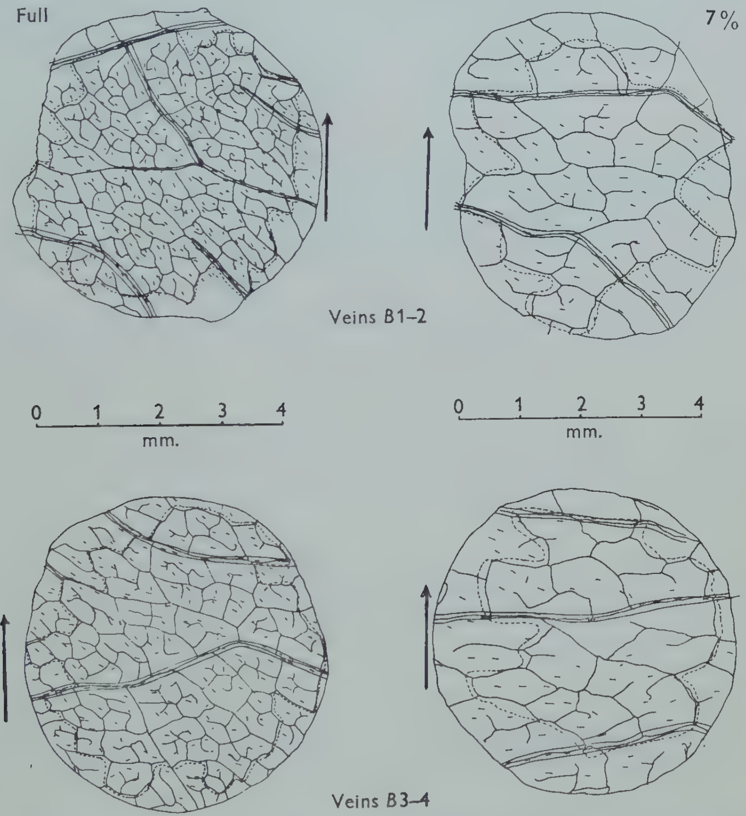

Fig. 3. Venation of mature intercostal region of 2nd alternate leaf. Left: full daylight; right: 7% daylight. Above: between veins *B*1 and *B*2; below: between veins *B*3 and *B*4. Arrows indicate the orientation of the mid-rib. Broken line encloses complete islets. Other dashes indicate crystal cells. Veins B 1, etc., are major lateral veins in basipetal succession as in Fig. 2.

This basic system of meristematic activity applies to leaves in all light climates, but the extent of expansion of laminae is inversely related to the total daily light radiation. This difference in expansion is clearly seen in Fig. 3 which compares the mature venation and crystalline inclusions of leaves developed in full daylight and in 7% daylight. The general pattern is the same, both with regard to the veins and the crystals, but the spacing is much wider in the shade leaf. The lengths of the leaves differed by a factor of about

1·8 and the areas by about 3·2, these figures corresponding to the difference in frequency of the veins and crystals.

The appearance of the mature lamina grown in full daylight is illustrated in Fig. 5, 1. The well-developed columnar palisade and the loose spongy mesophyll are characteristic of a sun leaf. A cell of the disjunct spongy mesophyll is seen abutting on the lower epidermis. For comparison the shade leaf is seen in Fig. 5, 2. Funnel-shaped palisade cells, together with a very diffuse spongy mesophyll, occur quite commonly in shade plants. The leaves are 270 and 100 μ thick, respectively, and the ratio of thickness is approximately the same as the ratio of dry weight per unit area of lamina. The complete structure of the lamina can only be illustrated by serial paradermal sections,[1] but one tissue of particular interest, the epidermis, will be described further here. Fig. 4 shows the epidermal cells of both sun and shade leaves at the same magnification. The shade leaf has larger cells than the sun leaf, but what is more remarkable is the difference in their outline. In general, the margins of the upper epidermal cells are less convolute than those of the lower, and likewise the cells of sun leaves are less convolute than those in the shade.

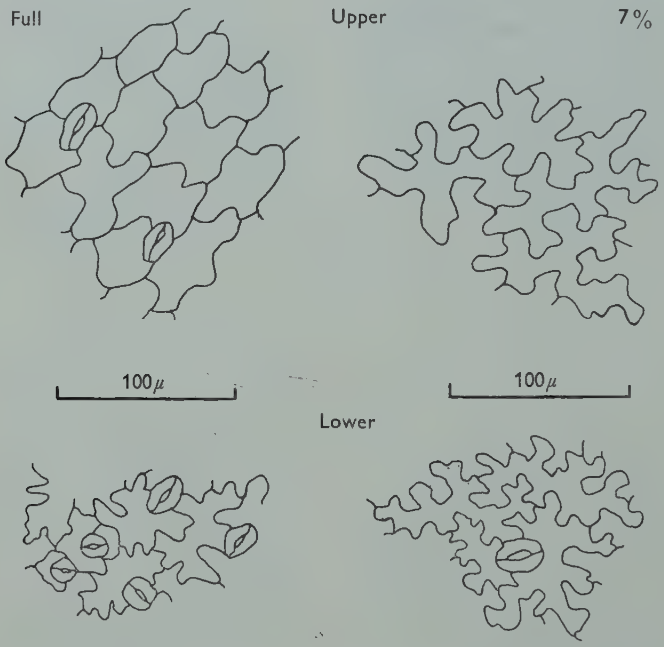

Fig. 4. Epidermal cells of 4th alternate leaf. Between veins $B1$ and $B2$. Left: full daylight; right: 7% daylight. Above: upper epidermis; below: lower epidermis

Before expansion there is little difference between the sun and shade form in the appearance of the lamina. In the section of a young shade leaf (Fig. 5, 3) can be seen the regular 'cobbled' appearance of the epidermis, the dense palisade with a crystal cell towards the left, two layers of ground mesophyll with a vein and its sheath differentiating on the right, and nearest the lower epidermis, the larger cells of the arm mesophyll with dense tanniferous contents. Examination of the lower epidermis in surface view shows that the stomata are differentiated in two flushes as the lamina expands. The 'cobbled' epidermal cells of the young lamina in paradermal view resemble those of the mature sun leaf both in size and shape. At a deeper plane, in the ground mesophyll layers, a complete closed pattern of veinlets is found. In mature leaves by comparison, blind ending veins are formed.

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[1] At the Symposium lantern slides of paradermal sections were shown, but they are not suitable for reproduction in this paper.

The general conclusion drawn from this work is that the sun and shade leaves of *I. parviflora* are fundamentally similar in meristematic activity and that the difference in structure at maturity lies in the greater expansion of the shade leaf. Both types of leaf exhibit basiplastic development with successive segmentation of procambial strands from the ground mesophyll. The problem of the precise nature of the expanding agent remains to be solved.

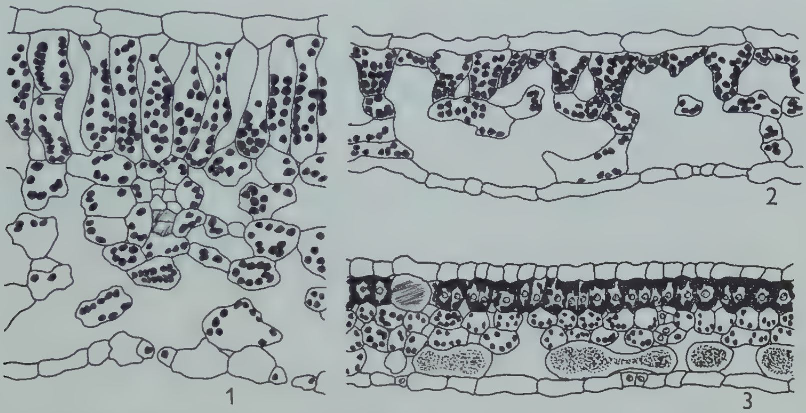

Fig. 5. 1, Transverse section of lamina in full daylight (270μ thick). 2, Transverse section of lamina in 7% daylight (100μ thick). 3, Transverse section of young lamina in 7% daylight (90μ thick). (All to same scale.)

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Some factors concerned in the growth of stolons in potato. By A. Booth. Department of Botany, University of Manchester[1]

(With Plates 5 and 6)

The potato used in this investigation was a variety of the species *Solanum andigena* Guz. & Buk. This plant was chosen for the reason that it produces tubers and flowers only when it is maintained under short-day conditions. In this respect it differs from most of the cultivated varieties of *S. tuberosum* L. as these have no absolute day-length requirement. *S. andigena* grows quite healthily under long-days; under these conditions stolons are formed, but tuberization does not take place. On this basis it is possible to regard tuber formation as the result of two separate processes, first, stolon formation, and secondly, tuberization of the stolons. In this paper some experiments bearing on the first of these processes will be described.

The plants were grown from tuber sprouts which, when rooted, were excised from the parent tubers and potted in John Innes No. 1 compost and maintained in a glasshouse at 60–70° F. with a day-length of 18 hr. Under these conditions single shoot plants were produced. The aerial shoot showed marked apical dominance and plants up to 4 ft. tall had no leafy lateral shoots. However, these plants did have stolons at their lower nodes.

It is well known that a stolon is a lateral shoot, developing at the lowest nodes of the plant, etiolated in appearance and bearing scale leaves. However, the physiological basis of stolon formation and growth is little understood. Two interesting questions arise: first, why do stolons develop at particular nodes; and secondly, and this is perhaps the more intriguing question, why do the stolons grow horizontally? The horizontal growth of stolons is not simply due to a lack of response to gravity, but is positive in nature. This is shown by experiments in which stolons are displaced from a horizontal position. Such stolons grow into the new horizontal plane.

Experiments relating to the first question, that is, why do stolons develop only at the lower nodes, will now be described. Stolons are initiated almost as soon as the shoot is formed (Pl. **5**, top left), and the question arises as to whether the stolons are laterals which grow out from axillary buds already laid down in the tuber sprout. To test this hypothesis stolon formation in aerial cuttings was examined. Aerial cuttings comprising the top 4–6 in. of plants about 1ft. high were potted in compost. They rooted readily and within a short time stolons were formed at the lower nodes. As these nodes were not present in the sprout this seemed to indicate that any axillary bud is capable of growing out as a stolon.

Stolon production in the young plant is restricted to nodes which carry adventitious roots and root development always precedes stolon formation. This also holds for aerial cuttings. A correlation was also observed between the amount of adventitious root growth of a particular plant and the number and length of the stolons formed. In plants with a more vigorous root system more stolon growth occurred.

An experiment was then carried out to investigate further this correlation between rooting and stolon formation. A number of plants about 18 in. high were lagged with moist, washed *Sphagnum* halfway up the stem. After three weeks the lagging was removed (Pl. **5**, top right). Roots were formed at the lagged nodes and at these nodes stolons had been produced. In no case was a stolon formed in the absence of roots.

Why should proximity to roots lead to stolon outgrowth? Briefly it would seem that this is not due simply to an increased local supply of nutrients taken up by the roots from the soil as the roots on the lagged plants were fed with water only. Thus one can postulate that either some more specific substance is produced by the roots which promotes stolon outgrowth, or that some feature of root attachment in some way favours lateral outgrowth. However, with regard to this last point, if one considers older plants it is found that stolons can be produced at nodes higher up the stem which do not have roots. Therefore, it would appear that the root stimulus is transmissible and is not due to local effects at the point of root attachment. Furthermore, a series of grafts was made in which aerial cuttings were grafted directly into non-dormant tubers. In this way it was possible to grow plants without roots. Stolons were formed in the absence of roots and the conclusion that might be drawn from this experiment is that the tubers themselves possess the root stimulus.

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[1] Present address: Botany Department, The University, Sheffield, 10.

Moving now to the second question, that is, why should the stolons grow horizontally? The first point to be established was whether or not light plays any part in the maintainence of the stoloniferous habit. Stolons are normally formed underground and it might be visualized that their etiolated appearance and possibly their horizontal growth is due to growth in darkness. However, in older plants stolons grow out into the light and remain etiolated and diageotropic (Pl. **5**, bottom right). These stolons have no phototropic response. When they are tied in a vertical position they curve and grow horizontally.

A second possibility was that correlative inhibition is in some way involved in stolon growth and this was investigated. In initial experiments plants were decapitated to determine whether or not the removal of the shoot apex and immature leaves released the stolons from inhibition. The result was that leafy lateral shoots were produced at the top three or more nodes of the plant and the stolons remained unaltered. However, when the plants were decapitated and the axillary buds of the aerial shoot were removed, the stolons responded by turning upwards and growing as normal leafy shoots (Pl. **5**, bottom left). In a second experiment the shoot was left intact and a single stolon was isolated from factors moving basipetally by making a transverse cut in the stem just above the point of insertion of the stolon. This stolon also turned upwards.

These results seemed to indicate that the suppression of leaf expansion and the diageotropic growth of the stolons is due to the action of some substance moving basipetally. In a separate investigation indole-3-acetic acid (IAA) had been found to be the only free auxin present in the potato plant. Thus it seemed reasonable to apply IAA to decapitated plants to see whether or not IAA would substitute for the intact apex with regard to its effect on stolon growth. In order to standardize the application of IAA halves of medicinal gelatine capsules were filled with a constant amount of lanolin paste containing IAA. These capsules were pushed on to the decapitated stems and resulted in a good contact between the paste and the plant tissue. With 200 and 500 p.p.m. IAA it was found that leafy lateral shoots grew out from the top nodes of the treated plants almost as quickly as in the controls which were treated with plain lanolin. In repeated experiments using IAA in concentrations up to 1000 p.p.m. not more than a slight delay in lateral outgrowth was effected. Thus IAA would not substitute for the apex in the inhibition of lateral shoot growth. This is an interesting point in itself as it might be expected that IAA would markedly inhibit lateral outgrowth.

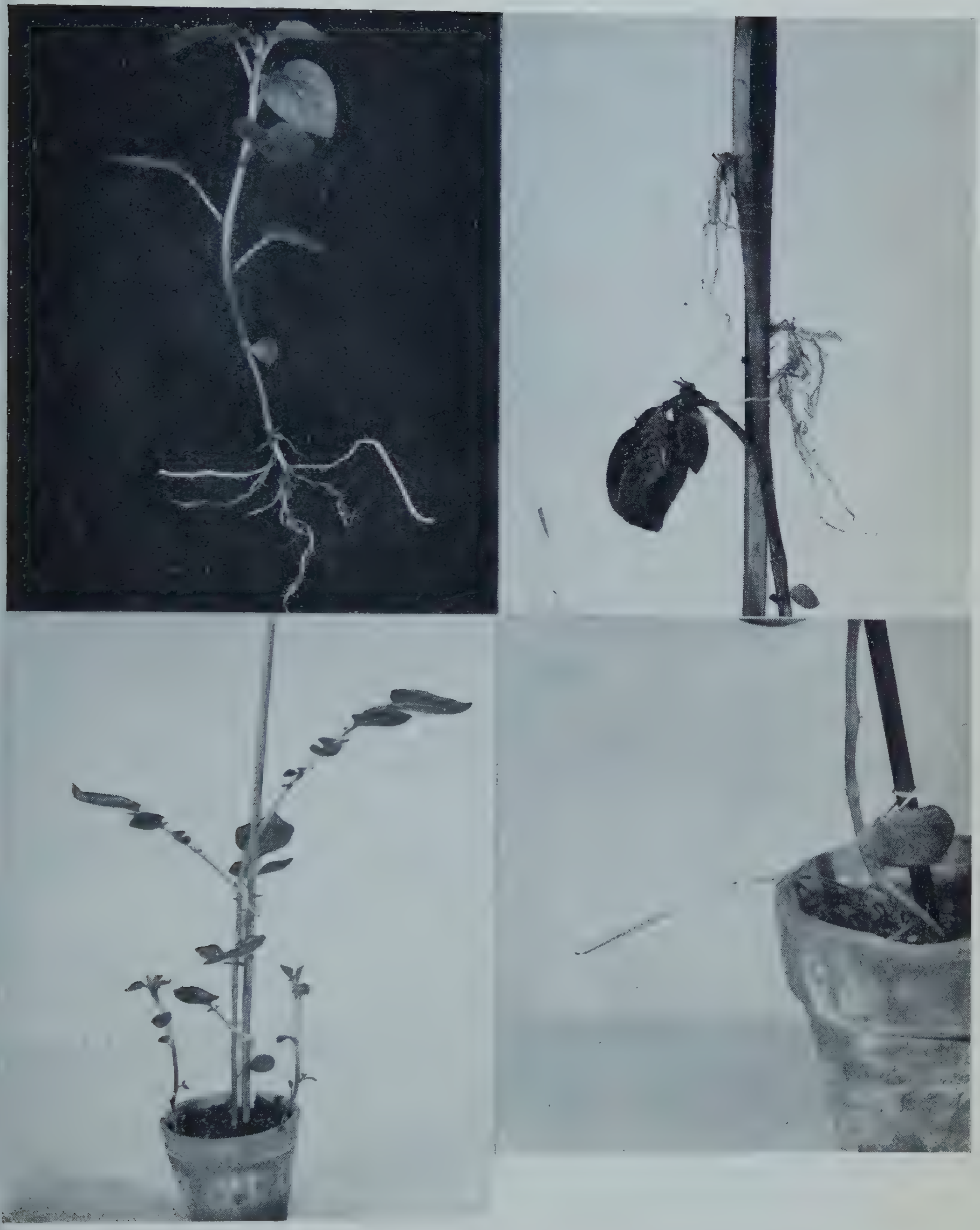
Two further series of experiments were then carried out. The first was to determine whether or not the application of IAA would prevent the stolons from turning upwards and becoming leafy shoots in decapitated plants from which the axillary buds of the aerial shoot had been removed. It was found that 500 p.p.m. IAA did prevent such a response. The second series of experiments was intially an attempt to inhibit the outgrowth of leafy lateral shoots from the upper nodes of decapitated plants. A mixture of 500 p.p.m. IAA and 1000 p.p.m. gibberellic acid (GA) in lanolin was applied to decapitated plants in an attempt to increase the inhibition due to IAA. The basis for this experiment was the suggestion that GA might act through a sparing action on endogenous auxin. This experiment led to a most interesting result. With IAA and GA together it was found that lateral shoots did grow out but they grow out as stolons (Pl. **6**, top left). The intact plant had no lateral outgrowths. In the plain lanolin controls leafy laterals were formed and these grew vertically upwards. With IAA alone leafy laterals were again formed, although in the initial stages of outgrowth the angle between the vertical stem and the lateral shoot was greater than that in the lanolin controls. With IAA and GA together the laterals grew horizontally and leaf expansion was suppressed. Thus with this treatment the laterals have every appearance of stolons. With GA alone normal leafy laterals were formed and these were more vigorous than the laterals of the plain lanolin controls.

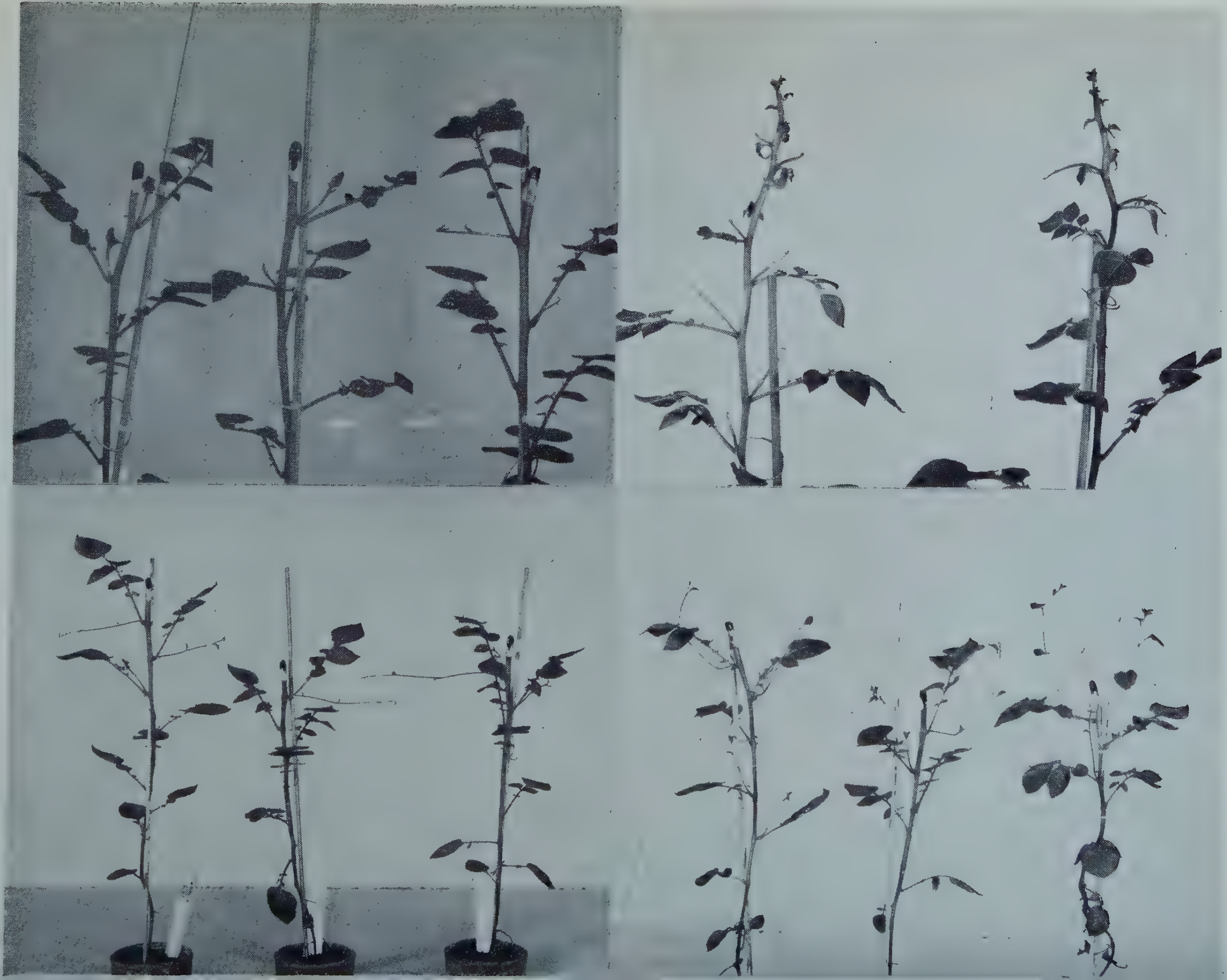
The action of IAA and GA together will now be described in more detail. It was found that within the first few days after the application of IAA and GA the mature leaves themselves responded by becoming horizontal. IAA or GA alone did not lead to this response. Later the leaves resumed their normal position at an angle of about 45° from the vertical. The laterals then grew out as stolons as shown earlier. Treated plants at a later stage have laterals several inches long which are perfectly horizontal and stolon-like in apearance (Pl. **6**, bottom left). Leaves are formed but they do not expand. In other plants of the same treatment recovery takes place in that the stolons turn upwards. This upturning of the stolons is closely correlated to leaf expansion (Plate **6**, bottom right).

How does a mixture of IAA and GA bring about its effect? Briefly, it would seem that two steps might be involved. It was mentioned earlier that IAA alone produces a small but significant initial increase in the angle between the vertical stem and the lateral shoot but that recovery quickly takes place. It might be held that IAA is responsible for the horizontal growth of the stolons. The difference between the treatments in which IAA alone was applied and that in which IAA and GA were applied together, might lie in the fact that IAA and GA together suppress leaf expansion. In decapitated plants treated with IAA alone leaf expansion takes place on the lateral shoots which grow out. It is well known that expanding leaves produce auxin. Thus in the treatment with IAA alone auxin produced by the expanding leaves at the tips of the lateral shoots may be responsible for the negative geotropic response of these laterals. It can thus be visualized that auxin is not produced at the tips of the lateral shoots of plants treated with IAA and GA, as the leaves do not expand, and therefore no geotropic response is given. This does not explain why the stolons grow so precisely horizontally but only why they do not become negatively geotropic.

A further observation may be held to support the view that auxin is closely concerned in the horizontal growth of stolons. It was found that normal plant growth did not take place when fluorescent lighting was used as the sole source of light. The shoot apex continued to develop and form new leaves but leaf expansion did not take place. In addition, lateral shoots developed at most of the aerial nodes and these had the form of stolons (Pl. **6**, top right). However, unlike normal stolons these grew out at an angle of 45° from the vertical stem. When such plants were returned to normal daylight expansion of the newly formed leaves at the shoot apex was resumed. Simultaneously, the stoloniferous laterals which had grown out at an angle of 45° from the vertical under fluorescent lighting curved downwards into a more or less horizontal position. The minute leaves present on the stoloniferous laterals did not expand and the downwards curvature of these lateral shoots might be interpreted as being due to the action of auxin produced by the expanding leaves of the main shoot apex. It was possible to reproduce the effect of returning the plant to daylight in plants maintained under fluorescent lighting by applying IAA in lanolin paste to internodes just behind the shoot apex.

In conclusion one can return to stolon formation in the intact plant. It would appear that stoloniferous growth is the result of an interaction between a 'shoot factor' and a 'root factor'. In so far as it is possible experimentally to produce stolons by the application of IAA and GA together it is tempting to suggest that in the intact plant such an interaction might be responsible for stolon growth. However the evidence for this is only circumstantial. It is proposed to describe and discuss this work at greater length in a further paper.





ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATE 5

Top left: a young plant showing the early initiation of the stolons.
Top right: a lagged plant with aerial roots and stolons.
Bottom left: a decapitated plant from which the axillary buds of the aerial shoot have been removed. Two stolons have become leafy shoots.
Bottom right: a stolon of an older plant growing horizontally in the light.

PLATE 6

Top left: decapitated plants with the addition of, from left to right, plain lanolin, IAA and IAA/GA.
Top right: plants grown under fluorescent lighting, the plant on the right returned to normal daylight.
Bottom left: plants treated with IAA/GA showing stoloniferous laterals.
Bottom right: plants treated with IAA/GA in which the stoloniferous laterals are showing recovery.

The study of apical development in relation to etiolation. By R. D. Butler and G. R. Lane. Department of Botany, University of Southampton

(With Text-figures 1–6)

The broad bean seedling, when germinated and grown in darkness, shows certain well-known differences from the normal; the lower internodes are excessively long (dolichotic), the leaves are small and yellowish, and the plumular hook is retained. The development, anatomy, and physiology of this etiolation syndrome has recently been studied in a number of plants and by a number of authors (Went, 1941; Parkinson, 1950; Thompson, 1950, 1951, 1954; Downs, 1955; Williams, Preston & Ripley, 1956); but little attention has been given to the shoot apex in any etiolated plant since Priestley studied it in the broad bean in the twenties. In the first place we have set out to ascertain by quantitative methods if the redistribution of growth from leaves to stem in darkness is reflected in a change of growth pattern in the stem apex. In order to obtain as complete a picture as possible, it has been necessary to carry out quantitative studies not only on the apical meristem itself, but also on the early development of primordia and internodes, in what we have called the subapical region.

The width and depth of the apical meristem were measured, together with the frequency and distribution of cell divisions within it. In the subapical region we determined the size, cell number, mean cell size, and the number of mitoses, of both primordia and internodes. The measurements discussed here were made from plants grown for 13 days in darkness and from controls grown in a 12 hr. day of artificial light, but younger shoots examined for comparison gave the same general picture.

Seedlings grown for 13 days in darkness (including a 24 hr. soaking period) bear shoots 25–30 cm. in length, the portion below the plumular hook possessing two or three elongated internodes. The two lower internodes are each three or four times the normal length. The total number of leaves and primordia is about nine, compared with eleven in the normal shoot of the same age.

The apical meristem was studied using both longitudinal and transverse sections. The width and depth of the apical dome changes, of course, with the stage of the plastochrone, but if the same stages are compared, no significant difference in dimensions can be detected between the normal and dark-grown meristem.

The frequency and distribution of cell divisions within the meristem were determined from camera-lucida drawings of sections. In the longitudinal plane, drawings were made showing the positions of mitotic cells in median sections. Twelve of these drawings, each from a separate meristem, were superimposed to form aggregate diagrams (Fig. 1). In the transverse plane a series of ten sections, each $10\,\mu$ in thickness, were cut from the tip of the dome, and the positions of mitotic cells marked in a single drawing. Eight of these were superimposed to form aggregate diagrams (Fig. 2). The same general picture is given by both longitudinal and transverse diagrams. The frequency of mitotic cells is lower in the meristem of the etiolated shoot. The lower mitotic frequency in darkness can reasonably be taken to indicate that the passage of cells through interphase is slower, for it is unlikely that growth in darkness would speed up the mitotic phase itself. It would thus indicate a slower production of new cells, and would account for the slower production of leaf primordia in the etiolated seedling. The relative distribution of mitoses is similar in normal and dark-grown meristems, divisions being more frequent in the region of primordium initiation at the side of the meristem.

Thus, growth in darkness appears to have no effect on the size of the apical meristem, nor upon the distribution of cell divisions within it. On the other hand meristematic activity, as measured by the frequency of mitoses, is less intense in darkness, leading to a slower production of primordia and internodes. These observations cannot be reconciled with the conclusions of Priestley and his collaborators (Priestley, 1926; Priestley & Ewing, 1923) that activity in the apical meristem of the etiolated broad bean shoot is confined to its basal regions, and that it is this which leads to the addition of more cells to the internode than to the primordium.

In the subapical region, measurements were made in the five youngest primordia and internodes. The basipetal succession from the apex represents a series of increasing age, and the measurements provide an indication of the changes that occur with time.

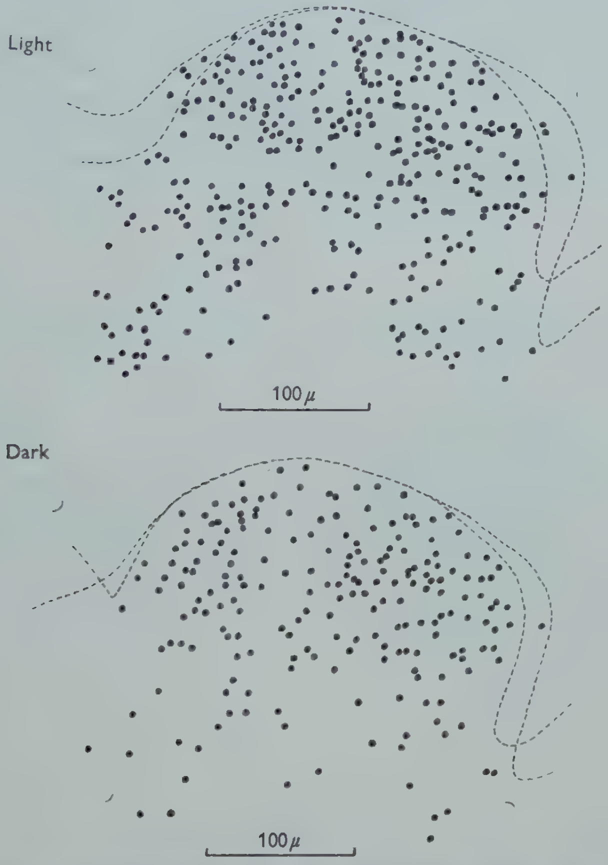

Fig. 1. Diagrams made by superimposing drawings of the median longitudinal section of the apical meristem of twelve normal and etiolated 13-day-old seedlings. Spots represent the positions of dividing cells. The outlines are those of the largest and smallest sections.

Primordia were examined by means of a maceration technique (based on that developed by Sunderland & Brown, 1956) which gave values for total volumes, cell number, mean cell volume, and the number of mitoses at the time of fixation. As is to be expected, a basipetal increase in all values occurs. The increase in mean cell volume and in number of mitoses is about the same in normal and etiolated shoots. On the other hand, the increase of both total volume and number of cells is greater in the etiolated shoot; the cell number of the oldest dark-grown primordium being about four times the normal value.

The internodes of the subapical region were examined using median longitudinal sections. Mean values were obtained for the length and breadth of each internode, the number of mitoses in the pith, and the number of cells along its length and breadth. As before, a basipetal increase in all values occurs, but in contrast to the corresponding primordia, the young internodes in the etiolated shoot are of normal size.

These results might seem surprising in view of the longer internodes and smaller leaves characteristic of the etiolated shoot. The explanation is quite simple. The apparent contradiction in the case of the primordia is due to the difference in the rate of production of new leaves and internodes in the normal and etiolated shoots which we have noted, and to the fact that six or seven primordia and internodes are already present in the ungerminated seed (Fig. 3). The slower production of primordia in the etiolated shoot means that each one has a longer development time than its normal counterpart. Moreover, the older dark-grown primordia were already present in the seed, and their growth period consequently extends back into the period of maturation. These two factors account for the larger size and cell number of the dark-grown primordia, and they mask a low growth rate. On the other hand, the fact that the young internodes in the etiolated shoot are of normal size despite these factors signifies that internode growth in the sub-apical region is indeed slower in darkness.

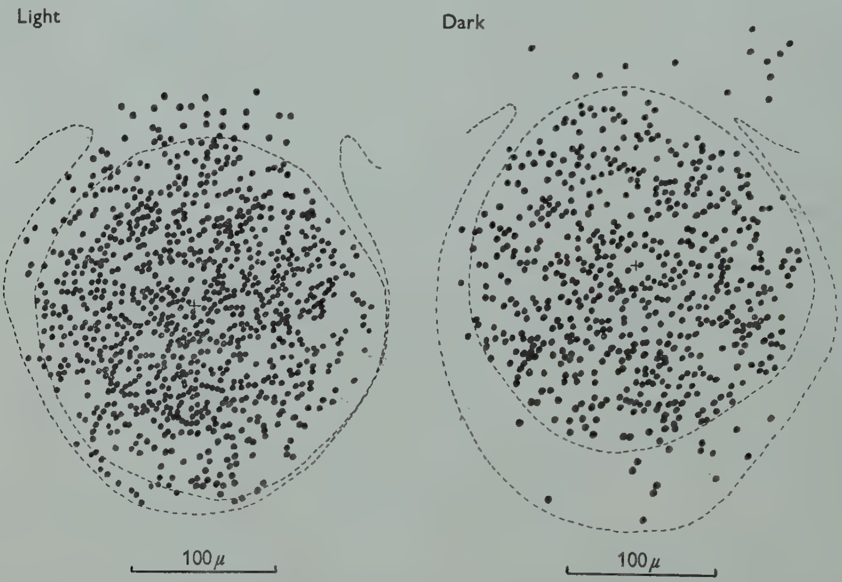

Fig. 2. Diagrams made by superimposing drawings of serial transverse sections of the upper 100μ of the apical meristem of eight normal and etiolated 13-day-old seedlings. The cross represents the axis, and the spots the positions of dividing cells. The outlines are those of the largest and smallest sections cut at a level 100μ below the tip.

Confirmation of these inferences is obtained by comparison of internodes and primordia in the normal and etiolated shoots taken in their order of production (i.e. numbered from the base of the seedling). The first nine primordia and internodes from the base are the only ones present in both normal and etiolated seedlings. This means that we can compare the three youngest in the etiolated shoot with the 3rd, 4th and 5th from the tip in the normal apex (Fig. 3). When compared in this way, both primordia and internodes in the etiolated shoot are smaller than the normal (Figs. 4, 5), the difference being due mainly to differences in cell number. These differences are partly the results of the slower production of primordia and internodes in the etiolated shoot, which gives them a shorter period of growth prior to sampling than their normal counterparts. This factor is most important when considering the youngest primordium and

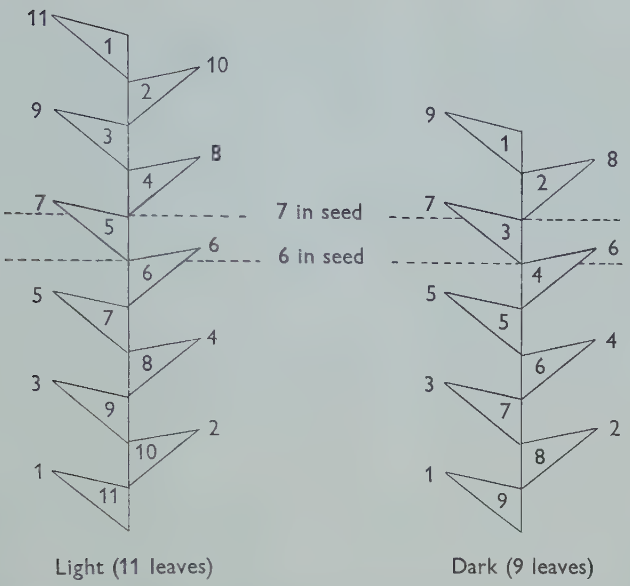

Fig. 3. Diagrammatic representation of normal and etiolated 13-day-old seedlings. Primordia and internodes below the horizontal lines are those already present in the seed.

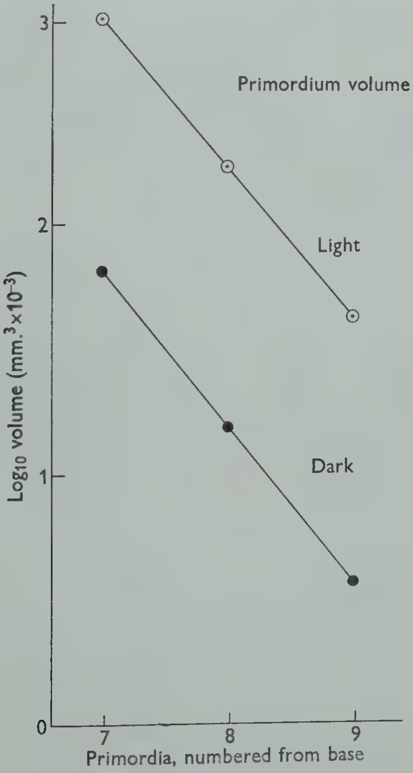

Fig. 4. Logarithms of the volume (mm$^3 \times 10^{-3}$) of successive primordia, numbered from the base, in the subapical region of normal and etiolated 13-day-old seedlings. Values are means of 8–15 measurements.

internode, for the difference between their time of initiation in the normal and etiolated shoot is greater. On the other hand, the seventh primordium and internode from the base are the first to be formed by the meristem on germination, and in some cases were already present in the seed. Their development time is therefore approximately the same in the normal and etiolated shoot. Nevertheless, this primordium and internode in the etiolated shoot are smaller than the normal, indicating a lower growth rate in darkness. This conclusion is supported by a lower frequency of mitoses in both primordium and internode. Evidently, the differences in measurements between light- and dark-grown primordia and internodes when examined in this way are due to a combination of two factors; (A) the slower production of primordia and internodes in the etiolated shoot, and (B) their slower growth in darkness once formed.

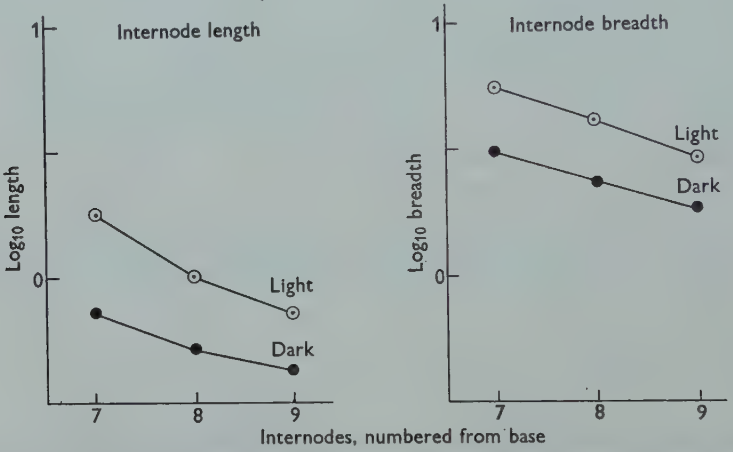

Fig. 5. Logarithms of the length and breadth (arbitrary units) of successive internodes, numbered from the base, in the subapical region of normal and etiolated 13-day-old seedlings. Values are the means of ten measurements.

Thus in the etiolated shoot, meristematic activity is suppressed in the apical meristem and in both primordia and internodes in the subapical region. It is clear that the redistribution of growth from leaves to stem in the etiolated shoot is not reflected in the stem apex. The characteristic symptoms of etiolation in the seedling arise solely in internodes and primordia already existing in the plumule of the ungerminated seed, and we have carried out experiments to determine at what stage it becomes sensitive to light.

In the first experiments (Lane & Butler, 1958) we determined the effect of a single 2 hr. light exposure, given at various intervals from the beginning of soaking, on the internode lengths and total height of dark-grown 13-day-old seedlings (Fig. 6). A light exposure given at 12–14 hr. gives rise to a reduction of about 15 % in the mean final length of the first (basal) internode, as compared with unexposed controls. Suppression of the first internode is accompanied by compensatory growth of the 2nd and 3rd internodes. Consequently, the effect of light is not revealed in the total height of the seedlings. From the results it appears likely that sensitivity may develop earlier than at 12 hr. Evidently, the plumule becomes sensitive to light immediately it has taken up water while the testa is still intact. This suggested to us that sensitivity may develop during the maturation of the seed, and that the light effect may survive until germination. To test this, seeds were matured, dried and grown in darkness, and the seedlings compared with controls matured in the light but grown in darkness.

Developing pods were enclosed in light-tight bags at an early stage, when they were approximately 1 in. long. Mature seeds from these pods were removed from the bags and dried for 10 days in complete darkness. Seeds from uncovered pods were dried under natural light conditions for the same period. All seeds were then soaked and grown in darkness, and internode lengths and total heights measured at 13 days. The mean length of the 1st internode from seeds matured in darkness turned out to be approximately 16 % greater than that from controls matured in the light. This difference is significant at the $P=0{\cdot}05$ level. It is clear that sensitivity develops at some time prior to final maturation of the seed. The light effect is able to survive a short drying process, and is revealed on subsequent growth in darkness. The mean length of the 1st internode from the light matured seeds does not differ significantly from that of the etiolated controls in the previous experiments, which were from commercially grown and stored seeds. It seems likely, therefore, that the effect of light can survive the usual long period of inactivity of the seed, and that the 1st internode of etiolated seedlings is always partially suppressed by light. We hope to verify this in due course.

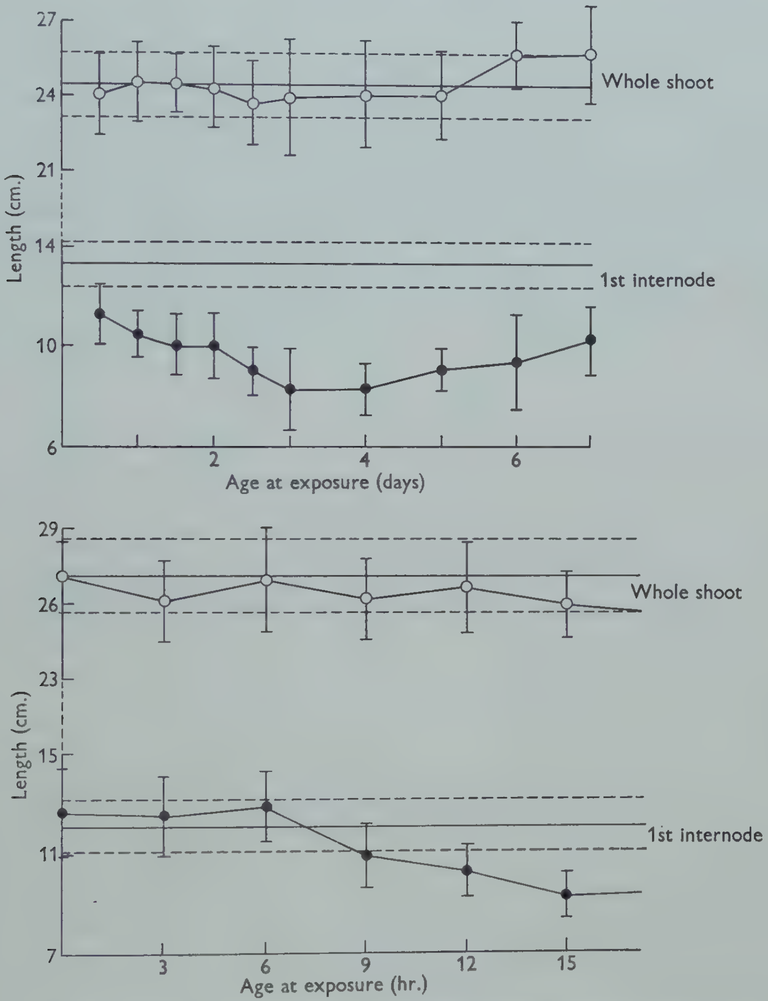

Fig. 6. Effect of a single 2 hr. light exposure on the first (basal) internode length (cm.), and total height (cm.), of dark grown seedlings at 13 days. The vertical bars indicate the fiducial limits at the $P = 0{\cdot}05$ level. The horizontal lines represent the dark control values and their fiducial limits. Values are means of 35–45 measurements.

The nature of the initial physiological effect of light has recently been discussed by

Williams (1956), and further speculation would be unprofitable at this stage. The effect clearly bears some resemblance to the vernalization effect on the embryo of winter rye, in that treatment is effective in the maturing embryo (Gregory & Purvis, 1938). An effect on the apical region of the rye plumule (Purvis, 1940) changes the whole growth pattern of the shoot, switching it from a vegetative to a floral pattern. Light falling on the plumule of the seed, or the tip of the etiolated shoot, immediately begins to switch the development from a 'juvenile' type, in which growth is mainly confined to young internodes already existing, to the 'adult' type in which growth is directed to the development of new internodes and to the expansion of leaves.

SUMMARY

Growth in darkness has no effect on the size of the apical meristem nor upon the distribution of cell divisions within it. On the other hand, meristematic activity is suppressed in darkness in both the apical meristem and the subapical region, leading to the slower production of primordia and internodes and their slower development once formed. The characteristic abnormalities in the etiolated shoot are not reflected in the stem apex. These abnormalities arise only in the lower parts of the shoot which were already present in the ungerminated seed. Sensitivity to light first develops during the maturation of the seed, and the effect of light is able to survive a short drying process. On germination, sensitivity is redeveloped before the start of cell division as the plumule takes up water.

ACKNOWLEDGEMENT

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Correlations. By L. J. Audus, Department of Botany, Bedford College, University of London

In 1880, Goebel wrote his masterly article on leaf morphology and growth and coined therein the term 'correlation' to include mutual growth-modifying influences between buds, leaves and stems. Later, in his *Lectures on Plant Physiology*, Jost (1907) extended this idea to such phenomena as wound healing and grafting, root and bud regeneration, etc. Particularly in the last two decades, progressively intensifying studies have further widened the field and have demonstrated the complexity of the phenomena involved. The tremendous expansion of our knowledge has led to a dismemberment of the subject and the development of its several facets into separate fields of study. In this way, the study of the control of flowering, of fruit growth, of abscission, of cambial activity, etc., have gone their several ways, and our vision of the underlying unity of the phenomena has been somewhat clouded. Nevertheless, it is now universally accepted that the control of the nature and intensity of growth in tissues, organ primordia and organs is brought about by a complex of growth factors, the majority of which originate elsewhere than in the cell where they ultimately act. Such action at a distance is characteristic of growth correlations between tissues and organs and is also one of the most fundamental aspects of morphogenesis. The study of morphogenesis then is largely the study of growth correlations and you will appreciate that my title leaves me the whole field of this Symposium over which to range.

Although it is my intention to discuss many experimental approaches which are relevant to the whole subject and to describe the achievements and also the deficiencies of some of the techniques employed, I can deal in detail with one aspect only. I have chosen therefore growth correlations between vegetative buds and between roots, that is to say mainly with the phenomenon of apical dominance. This is a subject which was among the earliest to be studied experimentally, but in spite of continued investigation over the years, the mechanisms involved are still very much of a mystery.

The control of lateral bud growth

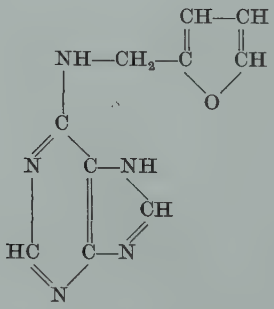
Introduction

We can perhaps distinguish three separate phases of bud growth. First, there is bud initiation, which includes those processes culminating in the appearance of the bud meristems. In the case of axillary buds, with which we shall be primarily concerned, their strict localization in relation to their associated leaf implies the action of correlative determinants emanating either from the leaf or leaf primordium or from the apical meristematic dome or from both. The second phase is that of the determination of the nature and number of the structures ultimately to be produced by the bud meristem. It might be supposed that this is not to be distinguished from bud initiation, but I prefer to regard it as a distinct phase, since there is no doubt that during these early developmental stages of bud growth the future course of development can be considerably altered by influences arising externally to the bud. The effect of temperature and day length in switching the course of development from vegetative to reproductive primordia is the most striking example of this kind of correlation. Lastly, there is the phase of expansion, when the growth is by cell volume increase. Many organ parts are here concerned and the spatial and temporal pattern of early expansion are complex and vary much from species to species. Often there is a period of inactivity between this phase and the previous one when little or no structural changes are going on. This bud dormancy is itself a complex phenomenon, being determined partly by intrinsic factors resident in the bud and partly by external correlative influences coming from other buds or from leaves. It would seem that the regulation here is mainly one of extension growth. Let us now consider each of these phases in turn.

Bud initiation

The factors concerned with the initiation of axillary buds have received little experimental study. Wardlaw, using the fern rhizome, has applied to the general problem of primordia determination, with which this is intimately connected, the techniques of microsurgery performed on the apical zone and primordia. This has demonstrated the existence of correlative determinants but so far has been unable to establish either their nature or their mode of action, although the most rational hypothesis postulates the existence of diffusable chemical evocators which, diffusing from several production centres, may produce complex interaction patterns which will determine the site of primordia initiation (Wardlaw, 1953, 1955).

Nevertheless, much has been discovered in recent years of the nature of bud determinants by the use of tissue culture techniques. Tobacco callus and stem tissue cultured in nutrient media under aseptic conditions *in vitro* may initiate adventitious buds. The rates at which buds appear on these tissue fragments can be used to assess the activity of suspected chemical determinants (Skoog & Miller, 1957). It has been shown that the hormone which controls stem extension, namely, indole-3-acetic acid, strongly suppresses bud initiation but that this can be counteracted by the purine base, adenine, which by itself promotes bud initiation (Skoog & Tsui, 1951). Bud numbers were further increased by phosphate in the nutrient medium. On the basis of such interactions, Skoog concluded that the old idea of a specific organ-forming substance, still perpetuated up to then in the guise of the various calines, should be abandoned and that the cellular conditions determining the initiation of a particular organ are set by a characteristic balance of a number of specific metabolites or growth factors. For buds, adenine, indole-3-acetic acid and phosphates seem to be the main components of this complex. Later, in an empirical research for further components of such determinant complexes, an impurity of commercial preparations of deoxyribosenucleic acid was found to have an amazing capacity to stimulate bud initiation, and showed similar interaction patterns as adenine with indole-3-acetic acid and phosphate. It was shown to be a close relation of adenine (i.e. 6-(furfurylamino)purine) with the following formula (Skoog & Miller, 1957):



Owing to its marked ability to stimulate general cell division in tissue cultures it was named kinetin.

Here, then, we have a system which could provide the mechanism both for the initiation and positioning of the lateral bud. If the leaf primordia were the source of one component of the complex, the apical dome of another, and perhaps the developing axis of a third, and so on, it is not difficult to imagine that an intricate pattern of gradients might be set up giving rise to the proper balance of the necessary factors for bud initiation in the axil of the leaf primordium. Similar conditions might control adventitious bud development but then the pattern would not necessarily be a regular one.

Unfortunately, as far as the details of this theory are concerned, kinetin still has to be found in higher plant tissues, although intensive search for it is in progress in Skoog's laboratory. The next logical step in the experimental development of this theory of chemical determinant interactions is the investigation of the spatial patterns of concentration of such chemicals in the relevant regions of the plant. This involves technical problems of such difficulty and complexity that it will be some considerable time before they can be adequately tackled. Some of the pitfalls of this experimental approach will be considered later. Another approach which has already shown promise, if correctly handled, is to apply chemicals which are suspected of interfering with the balance of natural determinants. Synthetic homologues of indole-3-acetic acid (e.g. 2, 4-dichlorophenoxyacetic acid) which do not come under the regulating action of the auxin, metabolizing system of the cell, and other homologues which are suspected of interfering with the natural auxin action, when applied to growing plants most certainly modify the development of leaf primordia and produce an amazing variety of abnormalities. So far as I am aware, their effect on lateral bud initiation and development has not been specifically studied. The effect of applying antagonistic homologues of adenine and kinetin might well be worth investigation.

Bud development and primordia determination

There is little doubt that the morphologically heterogeneous structure, which is the bud, develops under a complexity of growth correlations which may be both quantitative and qualitative and may act between organs in the bud, or between parts of the bud and organs on another part of the plant. As regards internal correlations we have already outlined the situation above when we were considering axillary bud initiation.

Correlative influences from outside the bud can determine both the extent and the nature of the subsequent growth of the branch structures arising from it. I must stress at this point that I refer here to influences exerted during the *development* of the bud up to the phase of dormancy and not to those affecting dormancy and the control of the subsequent release of extension growth. That the bud can be 'conditioned' during these early developmental stages has been clearly shown by Champagnat (1954) in *Sambucus nigra* L. Horizontal branches were taken and their orientation forcibly reversed so that the lowermost buds now became uppermost. If the reversal was performed in the summer (July), when presumably the buds were still 'plastic', then the uppermost buds extended most rapidly the following spring and produced the largest branches. If, however, the reversal was delayed until March, the lowermost buds (uppermost during the plastic period) produced the largest branches. Champagnat postulated the induction of 'propriétés fixées' by gravity during bud maturation. These properties determine the subsequent growth rate on bud burst. The most rational explanation of these effects is that gravity induces differential changes in the upper and lower sides of the main stem, which in turn modify the developmental processes going on in the young buds. It is tempting to think of the accumulation of an auxin on the under surface as the prime mover in this response. So far auxin is the only natural growth substance shown, by direct assay, to respond to gravity in this way, but I see no reason why other hormone systems could not behave similarly. So far they have just not been considered from this point of view.

The most striking and most studied of the qualitative changes induced by external correlative influences is the switch from the initiation of vegetative to the initiation of reproductive organ primordia during the onset of reproduction. Such changes we have already decided not to consider and they will in any case be dealt with elsewhere in this Symposium.

Bud expansion

Undoubtedly the differential expansion of buds and the branches to which they give rise determines the overall form of higher plants. Here the mutual correlative interaction of buds plays a central role. The situation, however, is complex and the behaviour differs widely from species to species, and, in perennial plants, within one species during its development. In herbaceous dicotyledonous seedlings such as *Pisum*, *Lupinus* and *Vicia* the apical bud growth dominates that of the laterals. This situation arises from a correlative inhibition exerted by the apical bud on the laterals, since removal of the apical bud results almost immediately in the onset of a rapid expansion in one or more of the laterals. A similar situation may be observed in young herbaceous shoots of woody perennials, for example, in *Syringa vulgaris* L., where a group of apical buds show growth dominance over lower lateral buds and the removal of such apical buds results, although usually after a long delay, in accelerated growth of the remaining lateral buds. This capacity to dominate is, however, acquired by the apical group during their early developmental stages, as is shown by experiments on gravitational influences (Champagnat, 1954). If shoots of *S. vulgaris* or *Prunus padus* L. are bent into a horizontal position during winter, then the terminal bud group still retains its apical dominance. If however, bending is done in the summer (June to August) then the subsequent spring growth of the terminal group is much smaller (one-half to one-seventh of the control) and buds lower on the main shoot produce correspondingly large branches. In woody shoots, for example of *Sambucus nigra*, the basal buds show dominant growth but the shoots they produce have no detectable inhibitory action on the slow-growing upper shoots, as appropriate debudding experiments have shown.

Here too, as we have seen in the previous section, the capacity for a subsequent rapid extension is acquired under correlative influences of the stem during the phase of bud development in the summer.

Research into correlative bud inhibitions has in the last 30 years been largely concentrated on apical dominance phenomena in herbaceous dicotyledonous seedlings and concerned particularly with the role of auxin in the phenomenon. Many enigmas surround this apparently simple situation, which is still far from being resolved.

In his pioneering studies Snow (1925), by 'grafting' experiments with *Phaseolus* seedlings, established that the inhibitory influence of the apical bud was transmitted by a diffusable chemical substance, since it would pass a watery gap. Later, when it began to be recognized that apical growing points were the centres of auxin production, Skoog & Thimann (1934) tested the hypothesis that auxin itself was the correlative inhibitor by applying solutions of it direct to the cut surfaces of decapitated seedlings. They showed that by this means lateral bud growth could be suppressed and concluded that auxin, produced in large amounts by the developing apical bud, was transported downwards to the lateral buds, which were directly inhibited by it. Thimann (1937) supposed that this response was based on the very high sensitivity of buds to auxins, so that concentrations which were optimal for developing apical shoots were supraoptimal and therefore inhibitory for buds. But Snow (1937) by an ingenious surgical experiment on twin-shoot *Vicia faba* L. seedlings, demonstrated that the inhibitory influence could pass in an acropetal direction along a shoot, thus arguing against a direct action of auxin, whose transport at that time was thought to be strictly polar and in a basipetal direction. Snow conceived the correlation inhibitor to be a special substance, not auxin, but in some way brought into being by the auxin flowing in the stems. Although other theories, which we have no time to consider, have since been put forward these two theories have stood centrally opposed and unresolved for the last 20 years. Let us consider some of the methods employed to tackle these problems and some of the more recent conclusions drawn.

The existence of a correlative inhibition acting both up as well as down the axis of shoots has been further established by decapitation, debudding, and defoliation experiments on a variety of plants. To quote one recent example, Libbert (1954*a*) has elaborated the technique of Snow and of Thimann and Skoog using *Pisum sativum* L. seedlings. Shoots were decapitated and the developing apical bud stuck back on the stump with agar. This allowed the release of lateral bud growth (an unexpected result in view of the earlier experiments of Snow). Later the apical shoot established tissue union with the stump and either the lateral shoot maintained or the apical shoot reassumed dominance, depending on the degree to which vascular connexions were re-established. In the first instance decapitation of a dominant lateral shoot allowed renewed growth of the inhibited main shoot, which then inhibited the growth of lateral buds on the lateral shoots. Application of indole-3-acetic acid paste to such decapitated lateral shoots reimposed inhibition in the apical shoot. This, and similar experiments, demonstrated unequivocally that correlative inhibition can be exerted both upwards and downwards in the same plant. But the situation differs from plant to plant, since in *Syringa* and in *Betula papyrifera* Marsh. the inhibitory action of leaves was shown by defoliation experiments to extend to buds higher up the stem, whereas in *Prunus padus* and *Sambucus nigra* L. the effects were strictly basipetal (Champagnat, 1955).

But we are no longer justified in arguing these theories on the basis of a strictly polar auxin movement. There is evidence (Jacobs, 1950; Leopold & Guernsey, 1953) that auxins can move even in extending tissues in an acropetal direction. Furthermore, many observations with tracer materials have now established that the synthetic homologues of indole-3-acetic acid move from leaves in the assimilate stream, and, although this is not yet established experimentally, there seems no reason why natural auxins should not do the same. On these grounds then indole-3-acetic acid is not ruled out as a direct correlative inhibitor of bud growth.

Another method of attack has involved the application, to experimental plants, of chemicals suspected of interacting with indole-3-acetic acid, in an attempt to block its movement or its inhibiting action. Tri-iodobenzoic acid, for example, on the basis of its effects on polarity phenomena, is suspected of inhibiting indole-3-acetic acid movement (Neidergang-Kamien & Skoog, 1956) while direct assays of indole-3-acetic acid from tri-iodobenzoic acid-treated tissues showed that this substance caused a great reduction in the auxin content (Audus & Thresh, 1956). It has been shown (Kuse, 1954) that ringing the petiole of *Ipomoea batatas* Poir. leaf at its mid-point with tri-iodobenzoic acid lanolin paste releases the axillary bud inhibition to the same extent as removing the leaf lamina, which argues for a direct indole-3-acetic acid action. Maleic hydrazide is a growth inhibitor which for a long time has been regarded as an antagonist of auxin action (Leopold & Klein, 1951), although it has no effect on auxin levels in inhibited plants (Audus & Thresh, 1956). When applied to plants in solution, it may release apical dominance and allow the growth of suppressed laterals, again supporting a direct auxin action theory. But recently it has been shown that the mechanism of maleic hydrazide inhibition may be by antagonizing the endogenous gibberellic acid (Brian & Hemming, 1957). This latter hormone, although it promotes bud extension after release from inhibition, seems to have little action in the inhibition itself (Wickson & Thimann, 1958). This illustrates the complexity of the situation and emphasizes the great dangers of using a suspected, yet incompletely established mechanism of growth substance action (here the antagonism of indole-3-acetic acid by maleic hydrazide) as a basis of, or check for, theories on other related phenomena.

An idea which played a large part in the work of the early pioneers of correlation, such as Loeb, was that competition for nutrients was the dominant controlling factor. In the modern hormone era this has been largely forgotten, although Went (1936) advanced the theory that the action of auxin in the dominant bud is to attract, in some mysterious way, other necessary growth factors, thereby robbing the laterals which have a much smaller auxin production. But although nutrient distribution may not be the whole story, there is evidence that it cannot be neglected. Gregory & Veale (1957) working with flax plants, have studied the effect of nitrogen and carbohydrate nutrition on the growth of lateral branches and their response to removal of the apical bud and stem tissues. Experiments with stem cuttings revealed that in flax there are gradients of 'growth potential' in lateral buds comparable with the 'propriétés fixées' of Champagnat. This growth potential is a maximum at the base (cotyledonary buds) and apex of the plant with an intervening minimum zone. Under conditions of high nutrition (nitrogen supply and carbohydrate synthesis) the growth of laterals takes place roughly in accordance with these inherent potentials, which anatomical investigations show are correlated with the ease with which vascular connexions between bud and main axis can be established. Under these conditions direct correlative inhibitions are negligible. Under restricted nutrient supply, lateral growth is confined to the vigorous buds, and the growth of weak buds is completely suppressed. Decapitation results in the increased growth of laterals, but since the absolute amount of extra tissue produced is the same irrespective of the state of nutrition of the plant, Gregory has equated this growth increase simply to the drain of nutrient materials by the apical bud. Furthermore, auxin application to decapitated plants under full nutrient conditions gave no perceptible inhibition of lateral shoot growth; in starved plants lateral branch growth was reduced to about a half by the high concentration of M/10 indole-3-acetic acid in lanolin.

There are observations that removal of apical buds may release lateral bud growth only in 'vigorous' plants, for example, in *Ginkgo biloba* L. (Gunckel, Thimann & Wetmore, 1949). In view of the above results on flax this is not surprising, since buds could not be expected to grow if nutrient supply were inadequate.

Gregory suggests that this auxin action is indirect and mediated by a suppression of the formation of vascular connexions to the bud, thereby robbing the bud of nutrient supplies. This reflects the earlier theory of Overbeek (1938) who imagined that a high auxin content in the stem maintained from the apical bud, in some way blocked the flow of nutrients to lateral buds and thus prevented their growth. The possible role of the vascular supply, its development and its efficiency in supplying growth factors of all kinds, has certainly been neglected in the study of correlation phenomena. In respect to auxin action, there is direct experimental evidence showing that it may be a determinant in vascular differentiation. For example, Camus (1949) has shown in root segments of *Cichorium intybus* that auxin application will, to some extent, reproduce the action of grafted buds in inducing the formation of vascular tissue in the parenchyma of this storage root. In *Coleus* stems Jacobs (1952) has demonstrated a similar action of indole-3-acetic acid in promoting vessel differentiation around a wound. Although these observations do not directly support the inhibition theories of Overbeek and of Gregory, yet they point the need for future work in this much neglected anatomical facet of correlative phenomena.

But more extensive experiments, using a wider range of indole-3-acetic acid concentrations, have shown that applied auxin is not always inhibitory to lateral buds. Ferman (1938) decapitated *Lupinus* seedlings and applied solutions of indole-3-acetic acid in cups attached to the cut stump. He found that inhibitions of bud growth occurred only with concentrations above one part per million; lower concentrations of the order of those normally occurring in plants actually accelerated growth. Ferman concluded that in such buds auxin was normally suboptimal, and not supraoptimal as proposed by Thimann. More recently *Phaseolus multiflorus* Willd. seedling buds have been shown to respond in the same way (Meinl & Guttenberg, 1954). It might be argued of course that decapitation and the removal of the source of auxin in the apex had brought about this low auxin level in lateral buds, but conclusions similar to those of Ferman have been reached by Libbert (1954*a*) using a different technique. With methods previously described, he induced growth inhibition of a regrafted main shoot by application of indole-3-acetic acid to the decapitated stumps of a grown-out lateral shoot. Indole-3-acetic acid wa then applied directly to the young leaves of the main inhibited shoot when its growth recommenced. From such experiments it would seem that in correlatively inhibited buds, auxin levels, far from being supra-optimal are indeed suboptimal.

Such contentions are supported by direct measurements of auxin concentration in buds under various inhibitory conditions. As early as 1938, Ferman showed that inhibited axillary buds of *Lupinus* contained less auxin, as assayed by the *Avena* test, than growing buds. This was demonstrated in decapitated plants in which two lateral buds had been allowed to develop and one assume dominance. Furthermore, lateral shoots inhibited by indole-3-acetic acid application to the cut stump of sister buds *contained less auxin* than the growing shoots of controls released from the correlative inhibition by decapitation of sister shoots. Van Overbeek (1938) decapitated *Pisum sativum* seedlings and showed that decapitation increased the auxin content of the upper lateral buds, and that application of indole-3-acetic acid to the stumps put up the auxin content still further, a result directly opposite to that of Ferman. Camus (1949) has made auxin assays of extracts of the apical and basal regions of *Cichorium intybus* root segments in which buds were regenerating. In this tissue, actively growing buds inhibited other smaller buds and the influence was strongest in the direction shoot to root. He showed that for the first 6 days the apical region, where buds afterwards developed, had much less auxin than the basal region, but later, when the buds had appeared and begun to grow, the auxin content rose equally steeply at both the apical and basal ends. He promptly concluded that auxin has no part to play in correlative inhibition. Along similar lines Champagnat (1955) has studied the auxin relations of *Syringa vulgaris* leaves which, when mature, exert strong correlative inhibition on lateral buds below them but not on their own axillaries. This inhibitive capacity sets in when the leaves reach a length of 9 mm. and is maintained then throughout the life of the leaf. Although the auxin concentration in leaves falls progressively as the leaf ages, diffusible auxin collected from the stem cut just below the leaves rises slowly to a maximum at a leaf length of about 7 cm., due presumably to the rapidly increasing leaf bulk over that period. But as the leaf continues to grow even this diffusible auxin declines to extremely low values at maturity. Like Camus, Champagnat thus inclined to the opinion that a separate hormone, not auxin, was the correlative inhibitor involved. Such a view would seem to receive considerable support from Thimann's (1954) comments that in *Ginkgo*, and probably in woody plants in general, not the leaves but the stem itself contains the bulk of the diffusible auxin in the shoot.

Such conflicting behaviour of endogenous auxins in the correlative inhibition of buds is, on the face of it, a very strong argument in favour of the views of Camus and Champagnat. But a word of warning must be sounded with regard to the techniques of auxin determination used, a warning which is relevant to the whole field of plant hormone physiology. All these assays were done on simple extracts or diffusates, which may contain a host of growth active substances, both stimulatory and inhibitory to growth. This will be well known to all who are familiar with the technique of paper partition chromatography applied to growth substance analysis. It is not impossible that the growth activity changes observed in such bud extracts may well be due to variations in inhibitor rather than auxin content. So far as I am aware, no attempt has yet been made in this particular problem of apical dominance to fractionate such bud extracts except by simple solvent partition which is, for all practical purposes, never complete and therefore misleading. A new approach to the problem using efficient chromatographic techniques and assays which are, if possible, chemically unambiguous, is long overdue.

Furthermore, the auxin assays described above have employed oat coleoptile tissue, which may, for all we know, be insensitive to some of the substances active in bud development. Kinetin immediately suggests itself. It seems logical then, if we are to avoid these pitfalls, to use the buds themselves as assay material in investigations of extracts, etc. This has indeed been done in the most recent experiments of Libbert (1954*b*), who worked with isolated nodes of etiolated seedlings of *Pisum sativum* supported in sand moistened with 2 % glucose solution. The inhibition of bud elongation on these nodes was used as a measure of activity of substances added to the glucose solution. Indole-3-acetic acid progressively inhibited bud growth from concentrations of 10 p.p.m. upwards. If roots were left attached to these experimental nodes, then bud sensitivity to auxin was greatly increased. Since the whole object of this investigation was to test Snow's special inhibitor theory, Libbert then applied the very popular inhibitor coumarin, and noted inhibitions at concentrations as low as 1 p.p.m. But more startling was the observation that in mixtures with coumarin the effectiveness of auxin was increased 100-fold by coumarin concentrations of 0·01–0·1 p.p.m. From this it was concluded that the special inhibitor of Snow probably arises from the interaction of auxin from the apical shoot with a coumarin-like unsaturated lactone from the root system, either by some kind of 'activation' of the lactone or by the formation of an auxin-inhibitor complex. From this point Libbert (1955*a*) began to test this theory by the assay of epicotyl extracts by his bud growth method, the assumption being that this was a specific test for the correlation inhibitor. First, the inhibitor, unlike auxin, was shown to be a neutral compound, and so capable of being separated from indole-3-acetic acid by the now classical bicarbonate-acid ether solubility technique. It was shown to be lost from epicotyls on decapitation and greatly reduced by the removal of roots. Lastly, he made extracts of roots and tested them alone and in combination with indole-3-acetic acid on his isolated budded nodes. Both indole-3-acetic acid (0·1 p.p.m.) and the extract produced slight bud inhibitions (5 and 1 %, respectively), but in combination the inhibition rose to 21 %. All this was taken as strong evidence for his special correlative inhibitor theory. Still using the bud assay technique Libbert (1955*b*, 1958) proceeded to investigate some of the physico-chemical properties of this special inhibitor and even claimed to have liberated indole-3-acetic acid from it by hydrolysis, thereby establishing it as a lactone-auxin complex. This is an imaginative piece of work but, experimentally, leaves much to be desired since its conclusions depend too closely on potentially ambiguous techniques, for example, acid-alkali liability and pea enzyme test for indole-3-acetic acid and the lack of absorption on charcoal to eliminate indole-3-acetonitrile as the inhibitor concerned. Furthermore, similar experiments by other workers have yielded contrary findings. For instance in *Mirabilis jalapa* L. seedlings the responses of lateral buds to decapitation and auxin treatments is unaffected by the removal of the roots (Vardar, 1955). In *Phaseolus multiflorus* bud growth is inhibited by coumarin applications but, in contrast to the strong synergism with auxin claimed by Libbert in peas, indole-3-acetic acid at 0·1 and 1·0 p.p.m. markedly *reduces* the coumarin inhibition (Meinl & Guttenberg, 1954). The whole situation then needs to be reinvestigated employing more rigorous and specific chemical methods before we can accept this special correlation inhibitor of Libbert.

Using a similar isolated node technique Wickson & Thimann (1958) have established that auxins inhibit bud growth only if applied *immediately* after excision. The fact that bud inhibition, once released, cannot be re-established by auxin suggests to me that irreversible structural changes in tissue might be involved, for example, the establishment of vascular connexions as proposed by Gregory & Veale (1957). They further showed that kinetin, when supplied with auxin in equimolecular proportions, would completely prevent the auxin action, and proposed that the release of bud extension is mediated, as bud initiation seems to be, by a balance of auxin and kinetin-like factors.

In view of all this evidence it must be concluded that Snow was right, although possibly for the wrong reasons, in rejecting auxin as a direct evocator of correlative inhibitions in buds. Auxin undoubtedly plays a part, but a somewhat indirect one in a complex system or systems whose exact constitution and the balance of whose components may vary from plant to plant or indeed from bud to bud. The elucidation of the behaviour of this complex system is a task for the future.

I hope I may be permitted at this juncture to point to what I regard as the necessary steps which must now be taken if we are to clear up the enigma of the action of auxin in apical bud correlation phenomena. Thus bud and shoot *development* as well as size must be studied. For example, in the great majority of studies on lateral bud growth, bud length or volume has been the sole measure taken. Since it is now clear that each phase of cell growth and each particular organ or organ part may require its own particular balance of a complex of growth factors, the importance of refining the present methods of observing and measuring bud growth must be stressed. Simultaneously, we must have thorough anatomical studies on the buds being influenced, so that details of histological changes, particularly the development of conducting tissue, may be correlated with the growth and other physiological measurements. In view of the warning from the work of Gregory & Veale, these investigations should be carried out under a wide variety of nutrient conditions. Then we must follow, with refined and rigorous chemical techniques, the behaviour of the indole auxins in all buds both apical and lateral, and in leaves under the various experimental conditions where correlative inhibitions can be induced or modified. This should be done with a range of plants showing different kinds of dominance, for example, the acrotony, mesotony, and basitony of Champagnat (1954). Lastly, the fate of auxin applied in decapitation experiments should be closely followed, if possible by the use of unambiguous tracer techniques.

THE CORRELATIVE INHIBITION OF ROOTS

The problems of root branching, which concern mainly the control of lateral root growth and the influence on it of the main apical meristem in tap-root systems, differ from those already discussed under bud correlations in that here we are dealing primarily with initiation phenomena. The morphology of roots appears to be largely the direct outcome of the temporal and spatial distribution of lateral root initiation.

The experimental study of root initiation has been much more intense than the similar study of buds. Stemming from the long-established empirical horticultural practices of propagation by cuttings, the investigation of the humoral factors controlling adventitious root initiation was among the first of this kind to be made, It was soon established that auxin was the main, although not the only, controlling factor. This has been verified by much subsequent work, in which the main technique has been the measurement of root-forming ability in cuttings of all kinds supplied, largely empirically, with a variety of suspected participants in the rooting reaction. This root initiator, or rhizocaline theory, was first proposed and subsequently elaborated by a pioneer in this field, Prof. R. Bouillenne, who now postulates three major components of the system. First, a specific root-forming factor, of the nature of an orthodiphenol is provided by the leaves. This interacts, under the catalytic action of the second factor, an enzyme located only in the cells of certain tissues (viz. pericycle, phloem, etc.), with a third factor, which is auxin itself. By such a three-factor hypothesis he accounts for both the well-known promotion of root formation by leaves, the response to an applied auxin and the localization of response to certain cells (see Bouillenne & Bouillenne-Walrand, 1955).

As far as the evidence for response to applied substances goes, auxins appear to stimulate lateral and adventitious root formation in the same way. But in the former it seems probable that yet another factor enters the picture, namely, that which mediates the correlative inhibition by the main meristem. When this meristem is removed from the tap root the intensity of lateral production is much increased and such a response could be explained by the action of a specific correlative inhibitor flowing from the main tip, an idea first proposed by Zimmerman & Hitchcock (1935) from studies on root decapitation of *Cissus*. Several other workers have since obtained similar results in other plants and have drawn the same conclusions from them.

The most comprehensive study so far made has been by Torrey (1950, 1956) in pea roots. 10 mm. root tips were isolated and grown under sterile conditions in a nutrient medium. Initial isolates could be induced to form laterals under the action of indole-3-acetic acid in the medium, but 10 mm. first transfer tips excised from these roots after 1 week were completely unresponsive and formed no laterals. Torrey concluded that, in addition to auxin, another substance or substances are needed for root initiation. These are normally provided by the cotyledons but are slowly exhausted in these isolated root segments. Following this he was able to show that the growth factors thiamin, adenine, and nicotinic acid all greatly augmented the root initiation action of auxins and to some extent eliminated the intrinsic acropetal root initiation gradients in isolated segments. One might suppose that the gradients of these accessory factors, established by flow from the cotyledons, might to some extent determine the sequence of root initiation in intact plants. In contrast to the situation with bud inhibitions kinetin has no effect on this rooting response.

But over and above this Torrey produced considerable experimental evidence that a rooting inhibitor from the root tip is also involved. For this he used 10 mm. excised tips of pea roots treated with 10^{-5}M indole-3-acetic acid solutions. In segments exposed to these solutions for 5 days root initiation could be easily observed in fixed cleared material under the binocular microscope. In one experiment these segments were each cut into two pieces at various distances from the tip and the root initiation was followed in each portion separately. In control uncut segments root initials were fairly evenly distributed between the apical and basal halves and, assuming a normal even distribution of this kind, I have calculated the net effect of this dissection on root initiation. Clearly the lateral root production by the tipless segment is far greater than that of the corresponding portion of the control tipped root, and the effective inhibiting part of the tip seems to be the terminal 2·5 mm., corresponding to the meristem and part of the elongating zone. In a search for the inhibitor proposed as responsible for this behaviour, Torrey made extracts of root tips with cold ether and investigated their effect on the indole-3-acetic acid response of root segments. He found a marked inhibition. During a recent visit to Dr Torrey's laboratory I was fortunate to be associated with him in further analyses of similar extracts with paper partition chromatography. The results, not yet published, indicate the presence of one specific inhibitor, which may differ from the already well-known extension growth inhibitors similarly isolated and assayed by the conventional extension growth methods. The next stage in this study is to identify this inhibitor, to follow its metabolism and distribution and thereby elucidate its role in lateral root determination.

Length of tip segment (mm.)	Total number of roots	Change in lateral numbers (observed minus calculated on an even distribution)	
		Base	Tip
0 (control uncut)	44	− 2	+ 2
1	35	− 5	− 4
2	51	+11	− 4
3	89	+38	+ 7
4	94	+40	+10
5	80	+31	+ 5

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The experimental investigation of the Pteridophyte life cycle. By P. R. Bell.

Department of Botany, University College, London

(With Plate 7 and 3 Text-figures)

Introduction

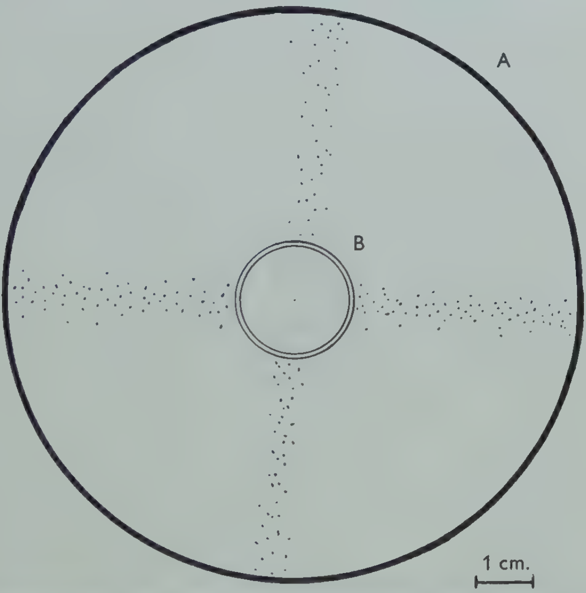
The identification of the factors responsible for the morphological cycle in Pteridophyta remains one of the most perplexing problems in causal morphology. It is some 50 years since Lang first suggested, arguing from the existence of isomorphic life cycles in the algae, that the reasons for the profound difference between the simple parenchymatous gametophyte and the complex differentiated sporophyte must be sought in the differences in the environments in which the initial cells of the two generations germinate (Lang, 1909). In those algae, such as *Dictyota*, where the initial cells of both the sexual and asexual generations germinate freely, unenclosed in any of the parent tissue, the two generations are identical in form and can be recognized only by their reproductive behaviour. As Lang realized, his hypothesis is open to experimental verification, but surprisingly little has hitherto been done in this field, largely because of the technical difficulties involved. An alternative hypothesis, advanced more or less simultaneously with Lang's, ascribed the difference in form between the two generations of the Pteridophyta to different determinants in the nuclei of the two generations (Blackman, 1909). Such a general hypothesis is not so open to verification as Lang's. A discussion of the relative importance of the nucleus and cytoplasm in the control of form follows after a review of the evidence at present available bearing upon Lang's hypothesis.

Experiments upon germinating spores and zygotes

By the use of pure culture techniques, facilitating the experimental treatment of gametophytes and embryos, it has been possible to go some way towards testing Lang's hypothesis, but much of the evidence for and against it is still indirect. The two crucial experiments which would determine the validity of the hypothesis once and for all are, first, to germinate a spore in the conditions in which the zygote begins its life, and, secondly, to isolate and allow a zygote to germinate in a free condition.

The first experiment would ideally involve injecting a spore into an archegonium, but it is difficult to see how this can ever be done for very simple reasons of size. Most fern spores are 30–40μ in diameter or least dimension, and the canal in the neck of an archegonium only about 15μ across. Rupture or removal of the neck and implanting the spore directly into the egg cavity, although not impossible for reasons of size, would hardly afford a legitimate test of Lang's hypothesis, since, as will be mentioned later, experiments have recently shown that removal of or damage to the neck above an ordinary zygote modifies the embryogeny in a remarkable manner. It is possible to inject a spore into the archegonial cushion of a gametophyte, but this is very far from providing it with the environment normally enjoyed by the zygote. The experiment has been tried many times with *Pteridium aquilinum* (L.) Kuhn, but so far, and not unexpectedly, with no results which would support Lang's hypothesis. Outgrowths of cylindrical form, eventually broadening to a cordate lamina, have often been obtained from injected gametophytes at or near the site of injection, but it has never been possible to show that these have originated from the injected spore, or even to identify the spore with certainty in the necrotic tissue bordering the site of injection. Moreover, outgrowths of this form frequently occur spontaneously from normal gametophytes or from gametophytes injected with water alone.

Albaum (1938) has provided good evidence for the existence in normal cordate gametophytes of gradients of growth-regulating substances. A strong gradient runs posteriorly from the base of the apical notch, and most of the archegonia arise directly in the path of this gradient. It has been argued that zygotes germinating in concentration gradients of this kind, and possibly also of a nutritive nature, are polarized by them and in consequence their development from the very beginning is switched into the path of sporophytic complexity. Not sufficient is yet known of the nature of the metabolites diffusing within the gametophyte to reproduce the natural gradients exactly *in vitro*. Nevertheless, it is known that a concentration gradient of indole-3-acetic acid reproduces some of the effects of those occurring naturally within the gametophyte (Albaum, 1938; Jayasekera & Bell, in preparation). Experiments were therefore set up in which spores of *Pteridium* were sown in a gradient of indole-3-acetic acid diffusing from a central source on an agar plate (Text-fig. 1). The results gave little of interest in relation to the problem discussed here. The concentration of indole-3-acetic acid adjacent to the ring wholly inhibited germination; midway to the periphery germination was poor and the differentiation disturbed, so that spores gave rise to nodules of cells instead of filaments (a well-known effect of indole-3-acetic acid in sublethal concentrations on germinating spores (Mohr, 1956; Soussontzov, 1957)). At the periphery germination and development were normal. Despite the fact that the concentration of indole-3-acetic acid must have fallen progressively along the radii in which the spores were sown, no constant relation between the direction of the gradient and the pattern of the development of the spores lying in it could be observed.



Text-fig. 1. *Pteridium aquilinum*. An experiment to determine the effect of germinating spores in a gradient of indole-3-acetic acid. (A) Petri dish containing 20 ml. Moore's medium solidified with 1·5% agar. (B) Glass ring placed on top of the original medium after solidification and containing 1·0 ml. of the same medium supplemented with 40 mg./l. indole-3-acetic acid. Further explanation in text.

Comparative morphology also yields an argument against the morphological complexity of the sporophyte being dependent *ab initio* upon concentration gradients within the gametophyte. In some species of the Schizaeaceae and Hymenophyllaceae the gametophytes are filamentous and clusters of archegonia are borne laterally quite removed from the direct path of any gradients within the body of the gametophyte. Nevertheless, so far as is known, the embryogeny of these ferns is similar to that of ferns with the familiar cordate gametophyte (Stone, 1958).

Lang's hypothesis, so far as it relates to the spore, remains unproven. The second crucial experiment the hypothesis demands, the isolation of a zygote, is certainly technically possible, given patience and skill. Although it has not yet been completely achieved, it has been possible to go a long way towards it. The experiments in question have been carried out on *Thelypteris palustris* Schott. Individual specimens of gametophytes were raised in pure culture and taken for experimentation when about 0·75 cm. or more long and fully archegoniate. An area of the archegoniate cushion, bearing 3–5 mature turgid archegonia and 0·5–1·0 mm. behind the apical notch, was selected under the microscope and dissected out from each gametophyte with the aid of a micromanipulator. The archegoniate surface of the portion of gametophyte so removed was approximately square and of the order of 0·2–0·5 mm. at the edge. These minute blocks were immediately transferred to suspensions of antherozoids obtained from thickly sown cultures of the same species. After 24 hr. each block was transplanted on to an agar slope and the behaviour followed. From fourteen blocks, about a third of those treated in this way, embryos developed. Even though the zygotes were removed from the influence of all but a minute portion of the parent gametophyte, the embryos were immediately recognizable as sporophytes, and no growth from these blocks not recognizable as sporophytes could be traced to a zygote. The development of the embryos arising in these isolated blocks differed from the normal only in minor features. For example, the rate of development (as measured by the emergence of the embryo from the calyptra) was reduced by about half as a consequence of the treatment, and the appearance of the first root was delayed even more in relation to that of the first leaf and stem. Undifferentiated basal tissue (the 'foot') also occupied a significantly larger portion of the volume of the young experimental embryos than normally (Jayasekera & Bell, in preparation).

In another series of experiments with *Thelypteris palustris*, the neck was removed from above a zygote before its first cleavage, but the gametophyte was not in any other way damaged. It is possible to recognize an archegonium in which fertilization has occurred by the cells at the base of the neck which, following fertilization, enlarge and possibly undergo some division, so that a collar is formed above the zygote, on top of which stands the unchanged upper part of the archegonial neck. The earliest at which it was possible to identify this collar with certainty in *T. palustris* was the third day after fertilization, 2 days before the average time of cleavage of the zygote. In three gametophytes the neck was successfully removed by a clean transverse cut at the level of the top of the collar, without any damage to the zygote beneath. In each of the gametophytes so treated the zygote developed into a parenchymatous mass, on the upper part of which leaves and then stem apices appeared. These structures are not dissimilar to those regenerated from the parenchyma of the cut rhizome of *Onoclea* by Wardlaw (1946) and by the author from portions of the rhizome of sporelings of *T. palustris* placed on agar. This remarkable modification of the embryology, also obtained in similar circumstances in *Phlebodium aureum* (L.) J.Sm. by Ward & Wetmore (1954), was attributed to the partial release, by the removal of the neck, of the constraint placed upon the expanding zygote by the tissues of the gametophyte. The results of these experiments are discussed in detail elsewhere (Jayasekera & Bell, in preparation); the point to be observed here is that although differentiation of the tissue deriving from zygote was delayed by the removal of the archegonial neck, it was not prevented, nor were the tissues ultimately differentiating anything other than clearly sporophytic in morphology.

At present, therefore, it can be said that although it is possible to modify in form and rate the development of a zygote by various treatments, normal sporophytic morphology is fairly rapidly obtained by the products of its division. Although, when the neck of the archegonium is removed, there is a conspicuous intermediate, more or less amorphous, parenchymatous stage before differentiation sets in, this in no way resembles the characteristic morphology of the gametophyte, as might be expected from Lang's hypothesis, nor has any tendency been observed for gametophytic tissue to arise from it. The conclusion seems inescapable that, contrary to Lang's hypothesis, the development of the zygote is in some way determined so that given adequate nutrition, it yields tissues which rapidly acquire the morphological complexity of the sporophyte. In those ferns with cordate gametophytes, the orientation of the dividing wall of the zygote, and consequently the spatial arangement of the first organs, almost certainly depends upon gradients within the gametophyte (cf. Wardlaw, 1955), but there is no evidence that these gradients are responsible for investing the zygote with the capacity for producing tissues able to acquire a higher grade of morphology. The manner in which complexity of development may be regulated is considered later.

THE STABILITY OF THE GAMETOPHYTIC AND SPOROPHYTIC MORPHOLOGY

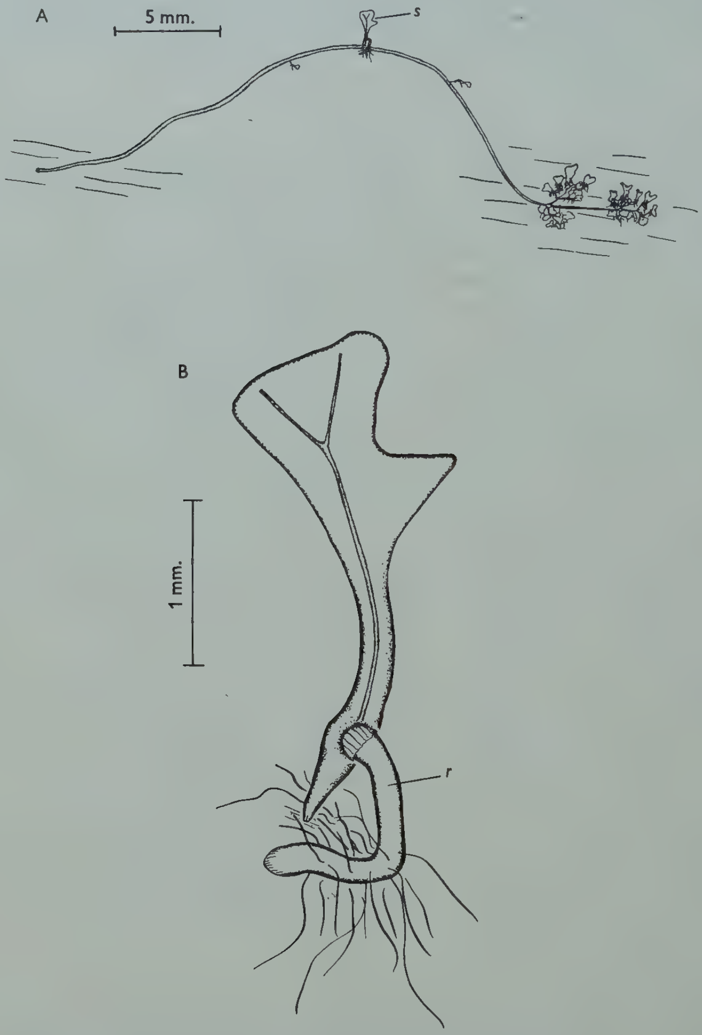
Although in the sexually reproducing ferns transitions from the morphological level of the gametophyte to that of the sporophyte and *vice versa* probably rarely occur in natural conditions, they can be experimentally induced.

A generally successful method of inducing apogamy is to allow the gametophytes to age without fertilization. The occurrence of induced apogamy (but possibly not the ability of the outgrowths to grow to maturity) appears independent of the constitution of the nucleus; for example, apogamous sporelings arise not infrequently in cultures of ferns, such as *Thelypteris palustris* and *Pteridium aquilinum*, which being simple diploids in the sporophytic phase cannot be suspected of hybrid origin. So far it has not been possible to cultivate these sporelings beyond a few leaves, but in *Phyllitis scolopendrium* (L.) Newm. a haploid apogamous sporeling has been successfully reared until it produced sporangia, when, as expected, meiosis failed and no spores were produced (Manton, 1950). Some species of *Lycopodium*, capable of normal sexual reproduction, give rise to sporelings apogamously very readily in agar cultures, but it has not yet been possible to raise these to the spore-bearing condition (Freeberg, 1957). There is no reason to believe that their behaviour at sporogenesis would differ from that of the ferns arising similarly without fertilization.

The reverse process, the aposporous production of gametophytes from sporophytes has also been frequently reported, but with the possible exception of *Osmunda regalis* L. (Lang, 1924), these observations appear to have been made principally on plants taken from collections, rather than from the wild (see, for example, Beyerle, 1932). Plants in collections may have genetic or physiological unbalance, resulting either from the selection of some decorative feature, such as cresting of the leaves, or from their being subjected to environmental stresses not normally encountered, and in consequence their behaviour may be abnormal. Accordingly, observations have been made on *Thelypteris palustris* and *Pteridium aquilinum* raised from spores collected from wild populations. Fully expanded leaves from young sporophytes were detached and placed in sterile conditions on mineral agar slopes (Bell & Richards, 1958). Almost without exception these leaves have eventually given rise to outgrowths of stable gametophytic form. It seems likely from these results that material tested previously was not abnormal and that the capacity to produce gametophytes aposporously is general in the ferns.

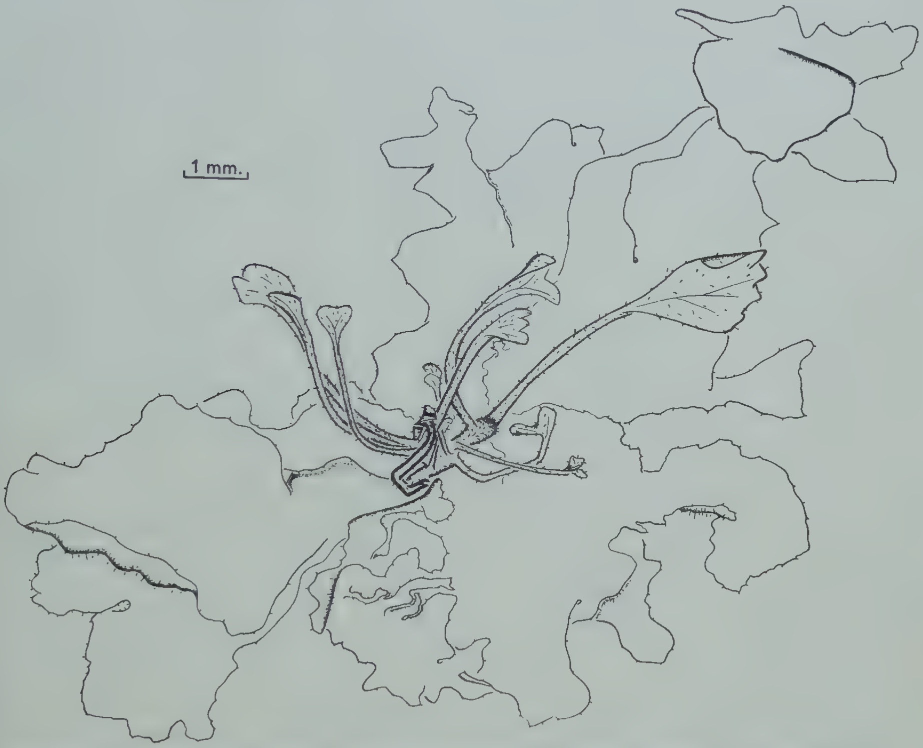
In certain conditions, a detached leaf will give rise to an outgrowth with sporophytic morphology (Text-fig. 2) (see also, Beyerle, 1932). The exact conditions in which this occurs, rather than the production of gametophytic tissue, cannot yet be specified, but it can be said that in the numerous experiments which have been carried out, not less than fifty in number, outgrowths from those parts of leaves in intimate contact with an agar surface have never been other than gametophytic in form. The one sporophytic outgrowth was obtained from the petiole rising from an inverted lamina, itself producing numerous gametophytic outgrowths. Duncan (1941), working with *Doodia caudata* also observed that gametophytes of normal form were obtained only from those parts of leaves in actual contact with damp *Sphagnum*; elsewhere the outgrowths were cylindrical and atypical. The significance of these results is discussed later.

It is of interest to note that the young sporeling of *Dryopteris borreri* Newm., an obligately apogamous fern, appears to be less stable morphologically than the young embryo of a sexually reproducing fern. The spores of *D. borreri* develop quite normally in sterile culture and the young sporophyte appears when the gametophyte is about 0·5 cm. long.



Text-fig. 2. *Thelypteris palustris*. Regeneration of both gametophytic and sporophytic tissue from the fifth leaf of a sporeling. (A) Position of the sporophytic outgrowth (*s*) in relation to the lamina which is lying on the agar surface and giving rise freely to gametophytes aposporously. (B) Detail of the sporophytic outgrowth: *r*, root arising endogenously.

Six young sporophytes of this fern, each bearing at least one fully expanded leaf, were dissected from the parent gametophytes and each placed upon 20 ml. of mineral-agar medium. Sexually produced embryos, if cut out at this stage, or even earlier, continue to grow quite normally on an agar surface, and any gametophytic tissue adhering to them undergoes no or very little proliferation. The behaviour of the *D. borreri* sporelings proved to be conspicuously different. Growth of the sporophytic tissue was very slow and eventually ceased, the successive leaves remaining juvenile in form and eventually dying. At the same time sheets of gametophytic tissue grew out from the base of the sporeling (Text-fig. 3). This gametophytic tissue produced no antheridia nor did it show any tendency to revert to the sporophytic form until it had been in culture for almost a year. A possible explanation of these results is that the morphology of the young apogamously produced sporophyte is not, like that of the sexually produced, firmly established. Both the up-grading and the down-grading of the morphology occur more smoothly in *D. borreri*, and possibly in other obligately apogamous ferns, than in the sexually reproducing.



Text-fig. 3. *Dryopteris borreri.* Behaviour of young sporeling placed on Moore's medium solidified with 1·5% agar. Explanation in text.

The facts of apogamy and apospory in the sexually reproducing ferns demonstrate not only that the transition from gametophytic to sporophytic morphology can be induced by appropriate treatment, but also that the transition can be reversed. Since these transitions can be brought about quite independently of sexual fertilization or sporogenesis, it follows that these morphological changes are independent of chromosome number. Moreover, measurements have shown that there is the same amount of deoxyribonucleic acid in the nuclei of aposporously produced gametophytes as in those of the parent sporophyte (Bell & Richards, 1958); consequently any change in the number of strands in the chromosomes, such as is known to occur in some regions of higher plants (Duncan & Ross, 1950; Hasitschka, 1956), accompanying the degrading of the morphology can be ruled out.

It is noteworthy that the gametophytes produced aposporously from sporophytes by experimental treatments show no tendency to revert spontaneously to the sporophytic form. Neither Lang (1924) nor Manton (1950) report any tendency for the diploid or triploid gametophytes of *Osmunda* to produce sporophytes apogamously. One example of an apogamous sporophytic outgrowth has occurred in a diploid gametophyte of *Pteridium* after 6 months' culture. This outgrowth, a simple leaf of limited growth, is quite similar to those produced occasionally by normal haploid gametophytes. We can conclude that the new level of morphology imposed by experimental means is no less stable than that of normal gametophytes.

THE RELATIONSHIP BETWEEN METABOLISM AND MORPHOLOGICAL CHANGE

It might be expected that one of the most effective ways of modifying morphology would be to interfere drastically with metabolism, either by stimulating or by retarding it. It is certainly very easy to disrupt the normal sequence of development in gametophytes by including various substances, such as sugars, indole-3-acetic acid and adenine, in various concentrations in the media on which they are grown, or conversely by omitting from the media any source of nitrogen. The gametophytes instead of developing in normal sequence from a filament to a cordate plate, either remain filamentous or develop into irregular nodules of cells. There is no firm evidence, however, that such disruption permanently impairs the morphological potentialities of the gametophytic tissue; similar aberrations occasionally appear in ordinary mineral-agar cultures and outgrowths of normal form can often be obtained from them on subculturing on the same standard medium (the 'type I' proliferations of Steeves, Sussex & Partanen (1955)). Occasionally irregular growth is continued on subculturing and the ability to produce outgrowths of normal form lost (the 'type II' proliferations of Steeves *et al.* 1955). This more permanent impairment of growth is accompanied by aberrations in mitosis, so that the nuclei in different cells have different chromosome numbers (Partanen, Sussex & Steeves, 1955). These variations in development in culture, although of considerable interest, are clearly not directly related to the regular alternation of form in the life cycle.

Although both Lang (1898) and Duncan (1941) believed that good illumination, and consequently enhanced photosynthesis was a contributory factor, it has not yet been possible to discover with certainty any nutritional treatments which will promote the apogamous development of sporelings in sexually reproducing forms. The coralloid proliferations described by Steeves and his co-workers (1955) of the gametophytes of *Pteridium aquilinum*, the main source of apogamous sporelings in this fern, appeared sporadically in cultures and the factors inducing them could not be identified, except that they became more frequent with the age of the culture. Numerous cultures of this fern have been raised by the author on media containing sugars, the precursors of nucleic acid, and indole-3-acetic acid, but with no evidence that any of these substances, singly or in various combinations, promoted apogamy. There is, however, a suggestion from *Thelypteris palustris* that apogamous outgrowths are stimulated not only as the culture ages, but also as the medium dries. A gametophyte of *T. palustris*, about a year old, was accidentally left on an agar slope open to the air of the laboratory. Some 4 weeks later, when the slope had contracted to about half its original volume, the gametophyte was found to be covered with sporophytic outgrowths apogamous in origin and more numerous than these had ever been observed before on a gametophyte of this fern (Pl. 7). It has not yet been possible to repeat this under controlled conditions, but the observations are of particular interest in view of Wettstein's (1942) investigations of analogous behaviour in the diploid gametophyte of the moss *Phascum cuspidatum* Hedw. The leaves formed when the culture was allowed to dry came to resemble sporogonia, and rudimentary sporangia were produced at their tips. On remoistening, subsequent leaves were of the normal gametophytic form. The experiment was repeated on the same plant so that the relation between the complexity of the morphology and the hydration of the culture was clearly established. Bauer (1956) has more recently shown that dryness of the medium promotes the apogamous development of sporogonia in a diploid race of another moss

Georgia pellucida Rabenh. It is known that substances with growth-regulating properties accumulate in the media upon which the gametophytes of both ferns and mosses are grown (Bell, 1958; Gorton & Eakin, 1957), and some sort of equilibrium must exist between the concentrations of the diffusing substances in the medium and in the tissues of the gametophytes. Partial drying of the medium may cause a shift in this equilibrium so that substances with morphogenetic properties re-enter the gametophytes and affect their development. It seems unlikely that the drying effect is a simple osmotic one, at least, in the ferns, since were it so it would be much more readily reproducible.

Substances with direct morphogenetic effect are known in higher plants (see, for example, Skoog & Miller, 1957). One of these substances, kinetin, is also known to promote nuclear division in the primordia which arise on the protonema and give rise to the leafy shoots in the gametophyte of the moss *Tortella caespitosa* (Schwaegr.) Limpr. (Gorton & Eakin, 1957). The existence of substances able to enter into the metabolism of plants and influence their morphology, together with the preceding circumstantial evidence, makes it not improbable that a substance or substances exist, naturally occurring in the metabolism of the fern, which will promote the apogamous development of sporophytic outgrowths from gametophytes. Such substances may be discovered when those which accumulate in the media upon which the gametophytes are grown have been isolated and identified.

As with the sexually reproducing ferns, no substances have yet been discovered which will promote morphological transition to the sporophyte in the gametophytes of the obligately apogamous ferns. With *Pteris cretica* L., the addition of a sugar, such as glucose or sucrose, to the medium, causes the sporophytes to appear earlier than in controls, but no evidence has been found of a diminution in the actual quantity of gametophytic tissue produced before the development of the protuberance leading to the sporophyte.

Although attempts to stimulate the production of the sporophyte directly from the gametophyte by nutritional means have met with little success so far, a sharp diminution in the supply of nutrients to the sporophyte certainly promotes the degrading of the morphology. The experiments already described in which the aposporous development of the gametophytes has been regularly induced, involve a treatment of this kind. The young leaves, detached and placed on agar, are not only dependent entirely upon absorption from the medium for their supply of minerals, but, since they are closely appressed to the medium, possibly subject to outward diffusion of metabolites and enzymes. It is very striking that in these cultures the outgrowths of gametophytic tissue have not appeared until the leaf or fragment of leaf was near death. By this time not only must correlation of the cells of the leaf have broken down, but also considerable autolysis of protein and modification of the cytoplasm must have occurred. It will be recalled, too, that Lang (1924) obtained gametophytes aposporously from *Osmunda* by drastically reducing the nutrition of the sporelings.

The fact that regeneration of sporophytic form has never been obtained from sporophytic tissue in intimate contact with an agar surface, but only from that some distance from it, becomes significant in view of the nutritive conditions which can be envisaged. The situation is perhaps comparable with that obtaining in orchid protocorms growing on an agar surface. The protocorm itself consists only of undifferentiated tissue and Went (1954) observed that the bud from which the fully differentiated plant arose always appeared in the protocorm at the point furthest from the surface of the medium. This, the point which would be least deprived of essential metabolites by diffusion into the medium, appears to be the only region capable of growth at a higher level of morphology. Also relevant is the recent observation by Bauer (1957) that the morphology of regeneration from the seta of the moss *Physcomitrium pyriforme* placed upon an agar medium depends upon the hydration of the medium, a factor which would influence the speed of outward diffusion from tissue placed upon it. With high concentrations of agar (4 %), the tissue regnerated assumed the form of a young sporogonium or remained as an undifferentiated mass of cells; only with low concentrations of agar (1·5%) did the regeneration assume directly the protonemal form of the gametophyte.

An explanation in terms of nutrition probably also holds for the results obtained with the young sporelings *Dryopteris borreri*. Removed from the gametophyte and placed on a relatively large volume of a simple mineral agar medium, the curtailment of their nutritive supply and the loss of metabolites by diffusion may be such that the level of metabolism associated with an advanced morphology can no longer be supported and the morphology is consequently degraded. That the young sporelings of *D. borreri* should react to metabolic stress in a manner different from that of the young embryos of a sexually reproducing fern must reflect a difference in physiology of great morphological importance.

Recently Hotta & Osawa (1958) have provided direct evidence of a relationship between the metabolism of the gametophytes of *D. erythrosora* (Eat.) O. Ktze., a sexually reproducing species, and the complexity of their morphology. From the analysis of samples of gametophytes at successive stages of development, they have been able to demonstrate a sharp rise in the amount of protein per unit dry weight of the gametophytes at the point at which the cordate plate begins to form at the tip of the simple filament issuing from the spore. Moreover, if the gametophytes are grown in the presence of certain amino acid analogues, such as ethionine and 5-methyl-tryptophane, which probably interfere with normal protein synthesis, the transition from the filament to the cordate lamina is completely prevented. This indicates that the protein synthesis is intimately involved in the change of morphology and that the increase in protein content does not merely reflect an increase in the number of small non-vacuolated cells at this stage. Other experiments show that the addition of 8-azaguanine to the culture medium also causes the gametophytes to remain in the filamentous form. This result is ascribed to the interference of the 8-azaguanine with the synthesis of nucleic acid, probably of ribonucleic acid. There is, therefore, evidence that the change from the filament to the cordate lamina in the gametophyte of this species involves rapid synthesis of protein, and possibly also of ribonucleic acid. The increase of protein is of such magnitude that it must accumulate predominantly in the cytoplasm and not in the nuclei.

An analysis of the treatments which bring about morphological change in the ferns (and probably in other Pteridophyta), together with the direct evidence provided by Hotta & Osawa of metabolic change accompanying morphological change, provides a background upon which a new hypothesis can be formulated to account for the Pteridophyte life cycle.

AN ASSESSMENT OF THE FACTORS CONTROLLING MORPHOLOGICAL COMPLEXITY IN THE PTERIDOPHYTA

A review of the experimental evidence available has led to the view that the development of the spore and the zygote must be in some way determined, even though the normal course of development can be disrupted by external treatments. It is now necessary to consider whether the innate control of development derives from the nucleus or the cytoplasm.

Although the ability of the nucleus to control growth and development is well established, there is evidence that the cytoplasm may also influence the form assumed by developing tissues, independently of the nucleus. For example, in both archegoniate and higher plants the products of reciprocal crosses sometimes differ in appearance (Wettstein, 1937) and even in the pairing behaviour of the chromosomes at subsequent meioses (Wangenheim, 1957). These differences can be attributed to the different maternal cytoplasms going to form the initial zygotes. There is clearly every reason to expect that the chemical and physical properties of the cytoplasm will have direct morphological consequences, for the cytoplasm contributes to the formation of the spindle, the apparatus which determines the plane of cell division (for a review of the origin of the spindle in plant cells, see Tischler, 1951). The directions in which cells divide and build up a tissue are of profound anatomical and morphological importance, because distinctive shapes, degrees of ramification, dimensions, and symmetry, all depend as much upon the direction of cell division as its extent. Size, in turn, may, by influencing the distribution of metabolites, determine the pattern of differentiation within a tissue (Bower, 1930; Wardlaw, 1952). Consequently, the accumulating evidence (see, for example, Mather & Jinks, 1958) that some variation in the properties of the cytoplasm independently of the nucleus is permitted in somatic tissue is of great importance for the student of growth and form.

There are grounds, therefore, for inquiring whether features of the cytoplasm may not control the complexity of morphology which a plant is able to achieve. This is not to deny the nucleus ultimate control, but to suppose that in *somatic* development the immediate control is exercised by the cytoplasm. There is some evidence from higher plants that this may be the situation. In a species of *Gardenia* described by Stewart (1924), for example, the lateral branches have a morphology markedly different from that of the main shoot. If the laterals are struck as cuttings, they form squat, irregularly branched, bushes, quite unlike the normal plant. The morphology imposed upon the lateral shoots must, therefore, follow from a permanent change in the functioning of their meristematic cells. This does not, however, appear to result from any modification of the nucleus, since the flowers are normally borne on the lateral shoots, and the seeds so far as is known yield plants of the normal composite morphology. The inference is that in normal development the cytoplasm of the cells of lateral meristems becomes in some way altered and that this alteration is reflected in the different symmetry of the lateral members.

The recent demonstration by Steeves & Sussex (1957) and Sussex (1958) that the primordia of the leaves of ferns continue to develop into leaves if they are detached and placed on a nutrient medium indicates that the characteristic form of these members is not due to continuous influences from the main axis. A change must have occurred in the cells of the primordium in its initiation so that their progeny build up an organ of dorsiventral, instead of radial, symmetry. Since the spores, which are produced on the leaves, ultimately reproduce normal plants, this change can not be in the nuclei. The most satisfactory hypothesis is that the change in the cells of the primordium leading to the dorsiventral symmetry is confined to the cytoplasm, and that the properties of the cytoplasm may be varied by internal factors.

There are reasons for believing that the alteration of morphological levels occurring naturally, or induced, in the ferns also has its immediate origin in cytoplasmic, rather than nuclear changes. The arguments can be grouped as follows. First, the estimates of deoxyribonucleic acid in the nuclei of gametophytes arising aposporously and in those of the parent sporophyte give no evidence of gross nuclear change accompanying the morphological degradation. Secondly, the evidence points to experimentally induced apogamy and apospory resulting from metabolic situations not normally encountered in the life cycle. There is no firm evidence that metabolic stress in any plant, applied either directly or by grafting, can induce nuclear change. Moreover, the experiment with *Thelypteris palustris* in which different parts of the one leaf regenerated sporophytic and gametophytic tissue would suggest a mutability of the nucleus quite contrary to the generally accepted view of its stability in the face of environmental fluctuation. Thirdly, the existence of the obligately apogamous ferns, in which the transition from gametophytic to sporophytic morphology is a normal feature in development, is a strong argument against the morphological changes being directly initiated by the nucleus. The up-grading of the morphology of these ferns after the gametophyte has reached a certain size is a smooth and continuous developmental process, not suggesting any abrupt nuclear intervention. That the morphological transition can be readily reversed in experimental conditions in *Dryopteris borreri* and other species (Steil, 1939; 1944) with subsequent regeneration of the sporophyte is further evidence against the nucleus being immediately involved.

On the other hand, it is very probable that by its general control of the cytoplasm the nucleus allows the morphological transitions of apospory and apogamy to take place with greater or less facility. It is well known that horticultural varieties of ferns often show these phenomena very readily, probably a result of genetic unbalance following artificial selection. The curious form of *Phyllitis scolopendrium* described by Andersson-Kottö & Gairdner (1936) is an excellent example of this effect. Also, the fact that hybrids between sexually reproducing and obligately apogamous ferns are themselves obligately apogamous shows the profound influence of the nucleus of the obligately apogamous species upon the cytoplasm of the sexual with which it becomes associated at fertilization. Nevertheless, it seems more in accord with experimental evidence to regard the function of the nucleus in somatic development as permissive, rather than determinative. It is envisaged that limits are set to the functioning of the cytoplasm, but within these limits variation, spontaneous or induced, may occur with quite striking morphological consequences.

The foregoing considerations lead to the conclusion that the cytoplasm determines the gross nature of the morphology acquired by developing fern tissue. It is not denied that, as hybridization experiments show, the nucleus is responsible for the fine features of each morphological state which distinguish individual species, but it is proposed that the alternation of morphological levels in the life cycle of the Pteridophyta is a reflexion of the different states and properties of the cytoplasm in each generation.

A RE-EXAMINATION OF THE EVENTS IN THE PTERIDOPHYTE LIFE CYCLE

If, as concluded in the last section, the cytoplasm is of importance in determining the level of morphological complexity, then, in the sexually reproducing ferns, there must be some mechanism by which the state of the cytoplasm is changed in the process of reproduction. The two stages of sexual reproduction, gametogenesis and fertilization, are examined separately, and it will be seen that the former has several features of significance to this inquiry.

So far as spermatogenesis is concerned, there is little that appears relevant. The antheridia are produced very early upon normal gametophytes, at a time when there is no tendency for sporelings to appear apogamously. Antheridia may even be present upon filamentous gametophytes, where, if the results of Hotta & Osawa (1958), already referred to, are of general validity, the protein metabolism is of a very low order. The spermatozoids themselves consist of little more than nuclear material. Oogenesis, on the other hand, is accompanied by several features of interest. First, archegonia do not usually appear until after the production of antheridia, when the gametophyte is more mature, and its protein metabolism probably more complex (Hotta & Osawa, 1958). Moreover, in cordate gametophytes, the archegonia appear just behind the apical notch, and it is significant that this is the region from which develop, in *Pteridium aquilinum*, the coralloid proliferations from which arise most frequently the apogamous outgrowths (Steeves *et al.* 1955). In the obligately apogamous ferns, the process which develops into the sporophyte also arises from the gametophyte in the region corresponding to the archegoniate cushion in the sexually reproducing ferns. Secondly, in oogenesis itself there is evidence of cytological phenomena which occur nowhere else in the life cycle. In *P. aquilinum* and *Thelypteris palustris* the nucleus of the egg in the very young archegonium is clearly visible and stains with Feulgen's reagent with an intensity only a little less than that of the somatic nucleus. As the archegonium matures, the nucleus of the egg expands to an irregular oblate spheroid with a major diameter of the order of 18μ and a minor (in the axis of the archegonium) of 10μ. As this expansion occurs the nucleus stains progressively less with Feulgen's reagent and at maturity the staining cannot be identified with certainty (Pl. 7). The volume of the nucleus of the mature egg cell is some twenty-five times that of the somatic nucleus, so that if the amount of deoxyribonucleic acid in it, and its capacity for taking the stain, were unchanged the staining would be considerably diluted. However, experiments with basic fuchsin in aqueous solution of an intensity adjudged by eye equivalent to that of the stain in the somatic nuclei show that it is still clearly visible when diluted twenty-five times. A subjective element inevitably enters into the matching of colours in a minute opaque object under the microscope and in aqueous solution, but it does look as if either the amount of deoxyribonucleic acid in the egg nucleus is less than that in the somatic nucleus, or that it has undergone some change so that its capacity to take Feulgen's stain is lessened. There is evidence of a similar situation in the egg nucleus of certain Angiosperms (Rowlands, 1954; Krupko & Denley, 1956). Whether deoxyribonucleic acid is in fact absent from these egg nuclei has yet to be demonstrated incontrovertibly, but there is clearly evidence of nuclear activity peculiar to the egg. It may be that the expansion of the egg nucleus (presumably due to the incorporation of cytoplasmic material), and the dilution and possible modification of its deoxyribonucleic acid are an indication of an intense interaction at this point in the life cycle of the sexually reproducing fern of the nucleus and cytoplasm. It is not unlikely that it is here that the cytoplasm begins to be modified and its capacity for supporting an up-graded morphology established. No cell, however, can multiply and give rise to a differentiated tissue unless it has an organized nucleus but the fact that the nucleus of the egg is strikingly ill-defined in comparison with the somatic nucleus suggests that the modifying of the cytoplasm of the egg is achieved at the expense of nuclear organization. The entrance of the compact nucleus of antherozoid, and its intimate association and fusion with the nucleus of the egg, should perhaps be looked upon as the event which is essential for the completion of the modification of the cytoplasm and the reorganization of the nuclear component. This accomplished, continued growth is possible (cf. Rowlands, 1954), and the zygote gives rise to tissues of sporophytic complexity.

On this hypothesis development of a sporophyte from an unfertilized egg (parthenogenesis) would be a very unlikely event, since the cytoplasm in the modified condition and an organized nucleus would not occur together. This would account for the striking fact that, although known in the Angiosperms, parthenogenesis is almost unknown in the homosporous ferns. It has been recorded only in certain horticultural varieties (Farmer & Digby, 1907), the life cycle of which is altogether abnormal. If material similar to that examined by Farmer & Digby can be traced, it will be of interest to see whether the staining of the egg nucleus with Feulgen's reagent is in fact similar to that of the somatic nucleus. No recent studies have been made of the parthenogenesis reported in *Marsilea drummondii* A.Br. (Strasburger, 1907) and *Selaginella* (Bruchmann, 1919; Goebel, 1915).

Relevant to the discussion of the events in the egg cell is a recent report by Mather & Jinks (1958) of experiments on *Aspergillus glaucus* Link, in which they have compared the products of sexual and asexual reproduction. Since they find considerably less variation amongst the products of sexual reproduction than amongst those of asexual, they conclude that in sexual reproduction the nucleus has a profound effect upon the cytoplasm, so that in each reproduction cycle the cytoplasm is restandardized, and many or all of the alterations that have occurred in it in somatic development eliminated. Although these authors are not concerned with the determination of morphological complexity, it is noteworthy that an entirely different line of inquiry should have led to the view that it is predominantly in sexual reproduction that the nucleus imposes organization upon the cytoplasm, whereas in somatic tissue the cytoplasm is permitted some variation in its properties and functions.

If gametogenesis and fertilization are the occasions when, in the sexually-reproducing ferns, an up-grading of the morphology is made possible by changes in the cytoplasm, then the converse process must occur at sporogenesis. The physiology of sporogenesis is as yet hardly investigated, but there is some evidence that it is encouraged by increasing the amount of carbohydrate available to the tissue. It is often observed, for example, that ferns in situations where insolation is considerable may be depauperate, but abundantly fertile. Also Sussex & Steeves (1958), working with a number of ferns, have shown that whether or not sporangia appear on leaves developing from isolated primordia in culture is markedly influenced by the sucrose content of the medium. Although the evidence is still conflicting, there are grounds for believing that the onset of the reproductive phase may depend upon the balance of the carbohydrate and nitrogen metabolisms, promotion of the former rather than the latter favouring reproduction. If the nitrogen metabolism is relatively depressed in the fertile fronds of ferns, then meiosis may well lead to spores containing a cytoplasm of which the proteins and ribonucleic acid are reduced both quantitatively and qualitatively to such an extent that recovery in the tissues developing from the spores is not immediately possible. This reduction would, on the hypothesis advanced earlier, be reflected in the simple morphology of these tissues.

If the foregoing be the situation in the sexually reproducing ferns, then in the obligately apogamous, since there is no indication of an interaction between nucleus and cytoplasm similar to that in the egg cell of the sexually reproducing, the cytoplasm deriving from the spore must be capable of progressive elaboration, facilitating a progressively more complex morphology of the tissues containing it. It is possible that the efficiency with which the cytoplasm is able to evolve in this fashion varies with the species, but comparative studies of this nature have yet to be made.

The number of sets of chromosomes in the nucleus of the spore appears to influence the ability of apogamous outgrowths to reach maturity. Gametophytes whose nuclei contain only one set of chromosomes rarely produce viable sporophytes apogamously, whereas in at least two species, *Dryopteris austriaca* (Jacq.) Woynar and *D. filix-mas* (L.) Schott, the nuclei of the gametophytes of which contain two dissimilar sets of chromosomes, comparatively vigorous plants have been produced in this way (Manton & Walker, 1954). Since these two species are allotetraploids, the comparative vigour of the apogamously produced sporophytes may be facilitated by the interaction of similar, but not homologous, chromosomes in the gametophytic nucleus. That obligate apogamy in *D. borreri* and some other ferns is associated with general genetic unbalance and is not determined by a simple genetic factor was shown by Manton's (1950) investigations. Although hybridizing experiments show that the apogamous condition is dominant, there is no form of Mendelian inheritance.

No explanation can be offered at this stage for the cytological irregularity, the formation of the restitution nucleus, which accompanies obligate apogamy and ensures that viable spores are produced having the same chromosome number as the parent. There is, however, some evidence that ribonucleic acid has an effect upon dividing somatic nuclei similar to that of colchicine (Allen, Wilson & Powell, 1950). If the metabolism of the obligately apogamous ferns is such that ribonucleic acid is progressively accumulated by the cytoplasm, it is possible that a continuation of this process might lead to effects upon meiosis. It is noteworthy that the behaviour of the sporogenous cells is very variable in the obligately apogamous ferns; in only a proportion of the sporangia are eight spore-mother cells formed, in the remainder various other irregularities occur generally leading to a breakdown of meiosis and abortive spores. Such a range of behaviour would be expected were the factor controlling it a component of the cytoplasm variable in quantity.

CONCLUSIONS

The purpose of this paper has been to indicate a new approach to the morphological problems of the Pteridophyte life cycle. The gametophyte and the sporophyte may be looked upon as two levels of morphological complexity. In proposing that they reflect different states of the cytoplasm, which can be accounted for in terms of cell chemistry, a hypothesis is advanced which, although speculative, accommodates the experimental evidence at present available, and may serve as a stimulus to future research.

Two lines of investigation immediately suggest themselves and both are at present receiving attention, although it is too early yet to report results. First, in the obligately apogamous ferns, since the transition from spore to sporophyte is not interrupted by sexual fertilization, a study of the protein and nucleic acids of the cytoplasm at various stages of development becomes a matter of great interest and importance. Those concerned with the problems of embryogenesis in the higher plants have also reached the conclusion that apogamous forms may yield information of great value (Steward & Pollard, 1958). Secondly, an elucidation of the events in the egg cell is imperative for it involves not only problems of development, but also those of the transmission of the genetic information by the female nucleus.

Causal morphology is entering an exciting phase, for the problems of growth and form are beginning to be resolved in terms of proteins and nucleic acids, the complex molecules of the living cell of especial biological significance. Because of the isolation of the gametophyte from the influences of the parent sporophyte in the Pteridophyta, members of this group may provide rather simpler developmental situations than the higher plants, and prove particularly suitable for investigation by the cell physiologist. Almost a century ago Hofmeister's elucidation of the morphology of the life cycle of the Pteridophyta proved the key which unlocked the mysteries of the life cycle of the higher plants. There are indications that the Pteridophyta may play a similar role today, and the discovery of the causal factors governing the morphological developments in the familiar Pteridophyte cycle facilitate the investigation of the rather more intricate cycle of the Angiosperms.

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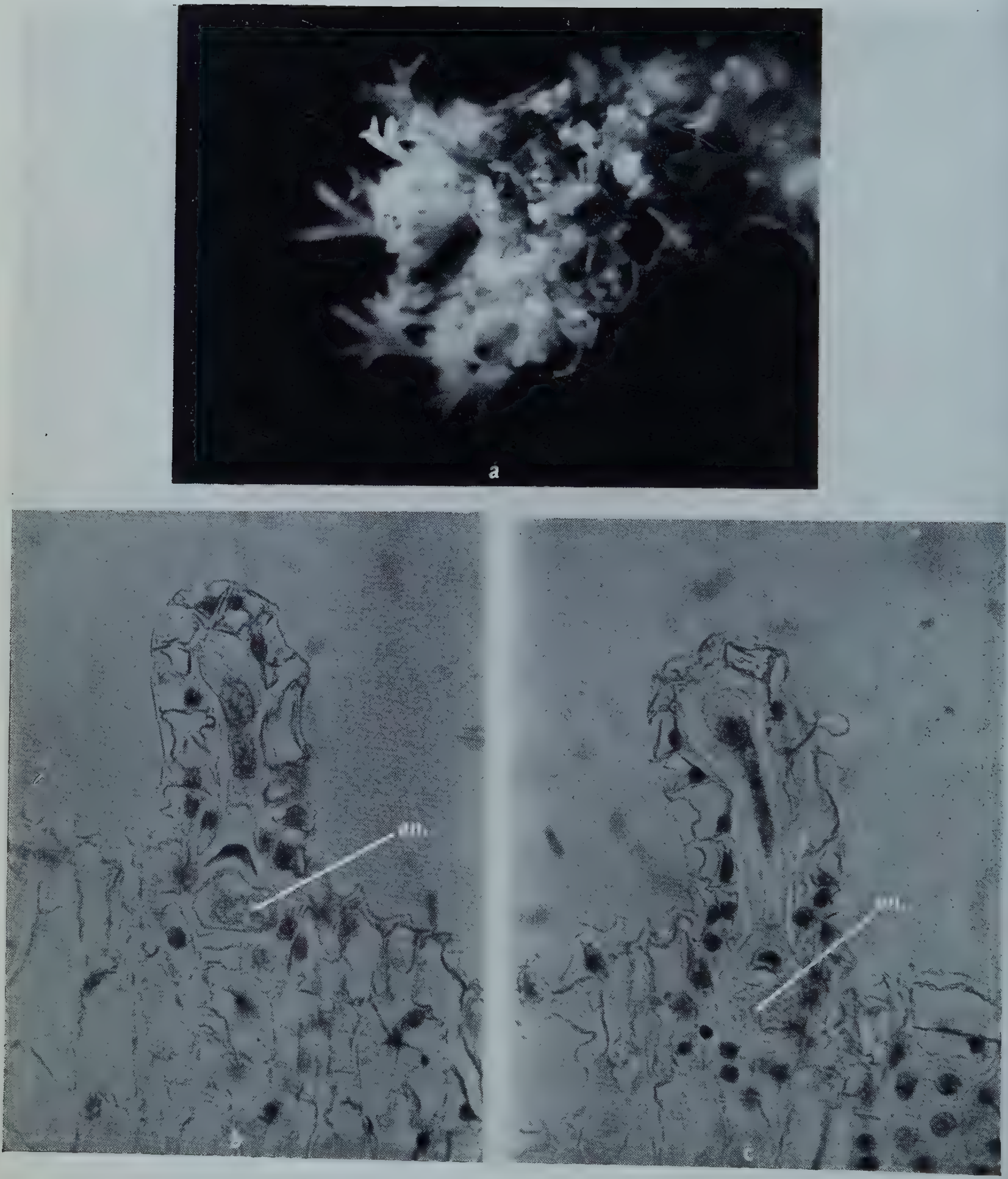
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EXPLANATION OF PLATE 7

(*a*) *Thelypteris palustris*. Portion of old prothallus covered with sporophytic outgrowths arising apogamously. (*b*) and (*c*) *Pteridium aquilinum*. Stages in the maturation of the archegonium stained in Feulgen's reagent. Each section, cut at 12μ, contains almost the whole of the egg nucleus (*en*.). The intensity of the staining of the egg nucleus diminishes as the archegonium approaches maturity.

Growth form and environment in Enteromorpha. By Elsie M. Burrows, Department of Botany, University of Liverpool

Most of the species belonging to the genus *Enteromorpha* have two apparently identical morphological phases in the life history, one which is thought to be diploid and the other haploid, though this has been confirmed in only a few cases. The diploid thallus develops from the zygote and the haploid from the zoospore and in both, in the early stages, a *Ulothrix*-like filament is formed. Longitudinal divisions lead to a two-layered filament and the layers separate early to form a tubular structure with a single-layered wall and closed above. In the very young stages growth is both by means of an apical cell and also by intercalary division, but the apical cell functions for only a short time. Attachment is by branched rhizoids, or sometimes by a definite horizontal disc, and from either of these systems new upright thalli may be formed by a change in direction of division of some of the cells. Branching of the upright thallus may occur and the branches appear to arise promiscuously from any cell, though the degree of branching appears to give a pattern sufficiently distinct for it to be used as a specific character. Reproduction may take place in any cell of the thallus except at the base or at the extreme tip. It involves successive division of individual cells so that a number, usually eight, of quadriflagellate zoospores for the diploid plant and biflagellate gametes for the haploid, are formed. Reproduction begins at the distal end of the thallus and progresses downwards, the tissues which have shed swarmers gradually being lost while new vegetative tissue is added by intercalary division below, this in its turn becoming reproductive and eventually lost. For a time vegetative growth exceeds loss by reproduction and the thallus grows in length, but the length of life of an individual frond may be as short as a few weeks.

Two points may be noted here:

(1) With the loss of the first reproductive tissue the apex of the thallus is also lost and the thallus becomes an open structure with only an intercalary method of cell division. It is still uncertain whether the apical cell has ceased to function by the time the first reproductive swarmers are formed, or whether there is any connexion between these two events.

(2) In culture experiments with a branched species of *Enteromorpha*, *E. compressa* (L.) Grev., I have found that lateral branches are already formed in the sporelings before the apical cell is lost, but whether it had actually ceased to function sometime earlier is again uncertain.

The recognition of species within the genus depends on combinations of the following characters: cell size within the thallus, cell shape, cell arrangement, chromatophore size in relation to cell size, presence and number of pyrenoids, degree of branching, and finally interfertility barriers.

It will be seen that several of these characters are likely to be affected by environmental conditions and experiments are in progress to determine the degree of variability of the characters under different conditions. It was during the course of this work that observations were made which might be of interest in the present symposium.

The evidence that I have been able to accumulate, often as isolated facts and small observations made at many different times, can be integrated at present into three main conclusions:

(1) In an alga with as apparently simple a construction as that of *Enteromorpha*, there is a physiological gradient from apex to base which shows itself in polarized vegetative and reproductive activity.

(2) The condition of the plants when collected from the field for experimental work is very important in determining the result of the experiments. This follows from the fact that the plants are able to exist in a very wide range of environmental conditions.

(3) Extreme changes in environmental conditions, such as cold shock or a great change in the salinity of the growth medium, may produce morphological changes in a plant comparable with those used as specific criteria.

The first two of these conclusions may be considered together.

The presence of a physiological gradient in the thallus is shown by the fact that swarmer production starts at the apex and progresses downwards towards the base while vegetative activity is largely at the base. Dangeard (1957), as a result of an experiment in which he cut fronds into pieces at right angles to the main axis and grew them in sea water, claimed that the cutting stimulated a proliferation of branches which was polarized. Rhizoidal filaments were produced from living cells bordering the cut surface on the lower side, while new *Enteromorpha* fronds were formed from living cells on the upper side. The conditions under which this experiment was carried out, the temperature, light supply and volume of water used, are not given. So far, I have been unable to repeat his results for two species with which he worked, *E. intestinalis* (L.) Link and *E. compressa* (L.) Grev., but as a result of my own experiments I am convinced that the conditions to which the plants have been subjected prior to experiment may be extremely important in determining their behaviour. Cultures raised under standard conditions from plants from a single field population at different times of the year have behaved in very different ways, in relation to such factors as growth rate and morphological appearance. There is no doubt that normally unbranched thalli can produce branches as proliferations of individual cells of the thallus. I have seen it in the field on many occasions and for several different species. There is another point, however, which needs to be considered here. *Enteromorpha* plants will live, as whole thalli or as broken parts of thalli, whether or not they are attached to a substrate, provided that they are at least periodically covered by seawater. If they are free-floating, then a distinction between apex and base has no meaning, and it may well be that polarized production of branches depends on the way in which the pieces of frond happen to lie in a culture dish rather than on the original orientation in the thallus.

My attention was drawn to this problem, particularly, by observations made on material collected from the field after a period of frost. Such material showed large thick-walled cells in the reproductive region of the frond, and these appeared to persist and grow out into new thalli after the remainder of the cells in this region had either shed their contents or died. Cells releasing reproductive bodies appeared to do so in the form of unusually large swarmers with more than the normal numbers of flagella.

Material of *E. compressa*, collected from the field at low tide in November, was stored at 2, 10° C. and at room temperature (about 20° C.) in plastic bags in dim light. When attempts were made the following morning to release swarmers, it was found that the plants stored at 10° C. and at room temperature behaved normally, releasing quadriflagellate zoospores or biflagellate gametes. The plants kept at 2° C., however, while liberating some swarmers which were normal, released many which were abnormally large and compound with multiple groups of flagella. In one or two cases, compound zoospores were seen in which the flagella were arranged in groups of three and five instead of the usual four. In double zoospores produced by this treatment, the two groups of flagella were sometimes at opposite ends, sometimes side by side, suggesting that the condition was the result of the incomplete separation of the cytoplast of the sporangium. It has been shown (Ramanathan, 1939) that plants of this species are monomorphic diplohaplonts (see Drew, 1955, for terminology), meiosis occurring in the zoosporangium. When the compound zoospores, produced by cold treatment, were formed, meiotic division of the sporangium nucleus may or may not have taken place. At least some of the zoospores will germinate, but nothing is yet clear as to their nuclear condition. If meiosis has occurred in the sporangium and the nuclei have separated completely, there is the possibility of the development of a gametophyte containing cells of different genetical types or, if such nuclei fuse, of the direct formation of a diploid plant. In either case the chance of survival for the species would be increased, on the one hand by a replacement of the dioecious condition by the monoecious and, on the other hand, by an elimination of the gametophyte generation. If meiosis has not occurred in the sporangium, then again the gametophyte generation would be eliminated from the immediate life history. The compound zoospore, if it can germinate successfully, could be an important structure in that it might enable the plant, which is normally dioecious, to eliminate this condition when adversely low temperatures prevail. The thick-walled cells formed in the reproductive region of the fronds of *Enteromorpha* plants in the field after a period of frost would appear to be the extreme limit of the above process in that swarmer formation is repressed altogether and the cells grow out directly to form proliferous branches. This is an effective way of vegetative propagation under conditions unsuitable for the survival of delicate swarmers.

The effect of low temperature seems to be, therefore, to replace reproductive activity by vegetative growth and the apparent effect is proliferous branching. This means that any specific criterion involving degree of branching has to be applied with caution. Whether the effect is produced by an absolute temperature or by a drop in temperature of a particular magnitude has not yet been determined. However, the latter of these two possibilities would appear to be the more probable, since plants collected in September when the outside temperature was more than 10° C., released compound zoospores whether kept at 10 or at 2° C. overnight, whereas plants collected in November, when it was much colder, released compound swarmers only after storage at 2° C.

Field evidence suggests that proliferous branching may also be produced by reduction in the salinity of the water in which the plants are growing. *E. micrococca* Kuetz. is an unbranched species, but is found in an excessively branched form under reduced salinity conditions (Setchell & Gardner, 1920).

We are in no position yet to discuss the mechanism of these processes, but it would seem likely that growth substances play an important part. Because of their relatively simple organization and the ease with which they can now be grown in culture, algae might prove favourable material on which to study morphogenesis.

Acknowledgement

I should like to thank Prof. N. A. Burges for his help in reading the manuscript of this paper.

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Experimental control of hyphal branching and branch form in hyphomycetous fungi. By N. F. Robertson, Botany School, University of Cambridge

(With 3 Text-figures)

Hyphomycetous fungi are either in fact, or by supposition, imperfect forms of the Ascomycetes and Basidiomycetes. Their 'spores' may be formed by simple fragmentation of the hyphae or, in a variety of more complex ways, by budding or by specialized growth at the hyphal apex. These spore-bearing parts are in turn borne as simple branches on the prostrate hyphae, or as terminal branches of an erect and often very beautiful branch system.

These branch systems, although characteristic for the taxonomist, are to some degree plastic with changing environment. It is well known to mycologists that fungi such as *Botrytis cinerea* Pers. and *Penicillium* spp. will fail to spore, or produce atypical conidiophores with few spores when grown in a saturated atmosphere; similarly that variations in the medium, in the incident light and in a variety of other environmental factors, may profoundly influence the shape of the conidiophore. Thus the genetic control of shape of the conidiophore is often closely linked to a particular set of environmental conditions and comparatively small changes in the environment upset the genetic control.

The control of shape in unicellular organisms poses problems which differ at least in degree from those in multicellular organisms with multicellular regions of differentiation. The Hyphomycetes which consist essentially of a string of cells left behind by a single apical cell pose problems which are similar to the problems in unicellular organisms for detailed development, but resemble those in more complex plants and animals in that there is an overall control of conidiophore shape. At first sight an analysis of the processes involved in the differentiation of the branch system and of the ultimate spore-bearing parts is too complex for present methods, although clues might be sought in changes in shape with changes in environment, but, if they have been, no general explanation of the mechanism of conidiophore differentiation has been given.

Another approach has been possible following observations on the behaviour of the hyphal apices of *Fusarium oxysporum* Schl. immersed in solutions of differing osmotic pressure. It was shown (Robertson, 1958) that the solutions used led to changes in the behaviour and appearance of the main growing hyphal apices on the agar plate. These changes may be summarized as in Table 1.

The explanation offered is that an alteration in the rate at which water enters the hyphal apex affects the whole mechanism of extension and may bring about arrestment. In an experiment in which the hyphae were immersed in water for from 5 sec. to 20 min. before being transferred to an isotonic solution it was clear that exposure of apices to water for 10 sec. was sufficient to bring about arrestment and the subsequent swelling and branching. What was more surprising was that when the fungus was exposed to water for 40 sec. or less, before being transferred to an isotonic solution, all apices swelled and branched, whereas exposure to water for more than 40 sec. before transfer to the isotonic solution led to about 50 % of branched apices, the remaining 50 % growing on from the apex of the slight swelling, as occurs in water alone. That is to say hyphae which swell a little and then quickly grow on from the apex, in water, become converted to hyphae which are arrested for 7 min. and show greater swelling and apical branching, if transferred from water to an isotonic solution within 40 sec. The explanation offered is that when the hyphae are growing normally the rate of extension is matched by the rate of wall-formation, or by irreversible changes in the primary wall some distance behind the apex and the growing apex of the hypha is still undifferentiated. Some of the hyphae when arrested by immersion in water rapidly reach equilibrium and grow on again within 40 sec. from the undifferentiated tip, whereas in others, which take longer than 40 sec. to achieve equilibrium and which remain arrested for more than 40 sec., the process of wall formation or the production of secondary changes in the primary wall continues into the undifferentiated region and the whole apex becomes covered by a 'set' wall which does not allow growth when equilibrium is achieved. New exit points have to be formed around the circumference of the apex and these take about 7 min. to achieve. The transfer of the fungus from water to an isotonic solution within

Table 1. *Behaviour of hyphae*

Treatment			
Water	Hypotonic solution	Isotonic solution	Hypertonic solution
Elongation stops	Elongation stops	Elongation continues	Elongation stops
Swelling of apex commences	Swelling of apex commences	No swelling of apex	No swelling of apex, slight shrinkage in strongest solutions
After 40 sec., about 50 % of hyphae grow on from tip of slightly swollen apex	After 40 sec., more than 50 % of hyphae grow on from tip of slightly swollen apex	—	No change visible
After 7 min. the remaining 50 % of the hyphae produce 1–6 (mostly 2) branches from the shoulders of the swollen apex	After 7 min. the remaining hyphae produce 1–6 (mostly 2) branches from the shoulders of the swollen apex	—	The apices recover their normal appearance and after a time greater than 7 min. (about 22 min. in 0·5 M. sucrose) produce 1–6 (mostly 2) branches from the shoulders of the apex

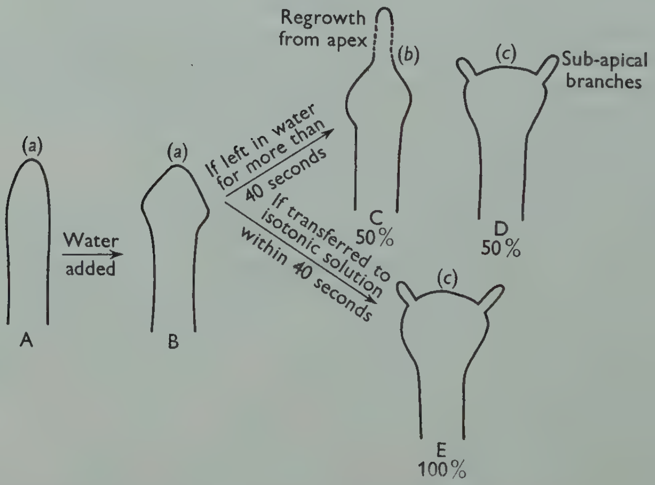
Regrowth from apex
(b)
(c)
Sub-apical branches
(a)
(a)
If left in water for more than 40 seconds
Water added
If transferred to isotonic solution within 40 seconds
A
B
C
50 %
D
50 %
(c)
E
100 %

Fig. 1. Diagrammatic explanation of behaviour of hyphal apices of *Fusarium oxysporum* in water and isotonic solutions. A, Normal hypha. B, Hypha showing arrestment and beginning of swelling. C, Hypha showing regrowth from the apex after immersion in water. D, Hypha which has swelled and branched at the apex after arrestment in water. E, Hypha which in water would have behaved as C above behaves as D above when transferred from water to an isotonic solution within 40 sec. of first immersion. It is suggested that the new equilibration following transfer maintains arrestment past the point at which the apex is incapable of regrowth. *a*, Undifferentiated apex; *b*, narrowing of hypha due to some wall differentiation; *c*, differentiated apex.

40 sec. necessitates two separate equilibrations and effectively prolongs the time of arrestment (even though only by a few seconds) past that at which irreversible changes in the apical wall take place. In Fig. 1 this proposed explanation is set out in diagrammatic form.

The interest of this phenomenon lies less in its special application to *F. oxysporum* than in the possibility that it has a general application as a mechanism of apical branching in the fungi. A survey has shown that the phenomenon of apical branching, following flooding of growing colonies with water, is widespread in the fungi. Thus it is shown by many species of *Fusarium* and by such widely differing fungi as *Rhizopus sexualis* (Smith) Callen, *Curvularia ramosa* (Bainier) Boedijn, *Trichoderma viride* Per. ex Fr. and *Thamnidium elegans* Link. Other fungi which did not show apical branching in water generally did so at some point, when treated with a series of concentrations of sucrose or sodium chloride in water. A more detailed investigation was made of one of these, *Neurospora crassa* Shear & Dodge. A white form of the fungus which occurred as a laboratory contaminant was used and the experiments were performed on 18 hr. cultures growing on plates of mineral-sucrose agar (Robertson, 1958) with the addition of 0·005 % Difco Yeast Extract. Because of the sensitivity of the hyphae of *N. crassa* extreme care had to be taken for the standardization of methods.

A detailed consideration of the results obtained will be left till a later paper, and for the purpose of this Symposium the results are presented diagrammatically in Fig. 2.

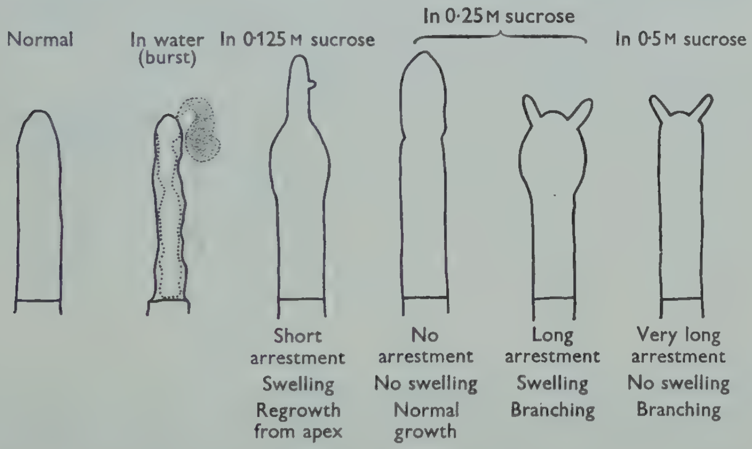

Fig. 2. Diagrammatic representation of hyphal apices of *Neurospora crassa* after treatment with water and sucrose solutions.

It can be seen that treatment with water causes bursting. With the other solutions arrestment follows flooding except in the case of 0·25 M sucrose where a proportion of the hyphae are so little affected by the solution that they grow on normally with only a slight indentation to mark the point of treatment. And in all treatments except that with 0·5 M sucrose some degree of swelling accompanies arrestment. This is further illustrated by the fact that the hyphae of *N. crassa* can be arrested and caused to swell and branch by making cuts across the agar plate either just behind the apices, thus severing the hyphae, or just in front of the hyphae.

Detailed examination of these results is not called for here but they are enough to indicate that the behaviour of the hyphae of *Neurospora crassa* differs in degree from those of *Fusarium oxysporum* rather than in kind, and that an explanation of their behaviour might be sought in the arrestment-swelling-branching hypothesis.

Observation of other fungi suggests that the sequence arrestment-swelling-branching on regrowth has a basic significance in fungal morphogenesis and forms a causal sequence. Observations of the development of the conidiophores of various *Fungi imperfecti* and reference to published figures of mature structures suggest that the sequence observed under experimental conditions on flooded plates is also followed in the development of conidiophores and other fungal fruiting structures.

In the simplest example arrestment is followed only by swelling. This can be seen in the sporangia of *Mucor* spp. and *Phycomyces* spp. In the beautiful time lapse photographs of Phycomyces (Castle, 1942) it can be seen that extension of the erect sporangiophore stops just before swelling of the apex takes place. Aberrant swellings showing regrowth and branching in Phycomyces sporangiophores are figured by Middlebrook & Preston (1952). In the *Fungi imperfecti* swollen conidiophore apices bearing many to few spores or branches can be seen in *Oedocephalum* spp., *Fomes annosus* Fr. (imperfect stage) and *Aspergillus* spp. Some swelling at the point of dichotomous branching can be seen in *Penicillium* spp. and in practically every dichotomously branching member of the Hyphomycetes (e.g. Figs. 11, 50 and 51 in Hughes, 1953). Another example of the swollen hyphal apex followed by branching can be seen in the basidium. The formation of a rigid cap on the basidial apex and the extrusion of the sterigmata as four subapical branch buds has already been postulated by Corner (1948) on observational grounds and it is true to say that the early stages of the events postulated by Corner can be mimicked experimentally in Fusarium and Neurospora. Yet another example can be seen in the spores of the aquatic hyphomycete *Heliscus longibrachiatus*, the development of which has been studied by Ingold (1945). Three of the arms of these tetraradiate spores develop as buds on the swollen apex of the fourth. Some of these examples are shown in Fig. 3.

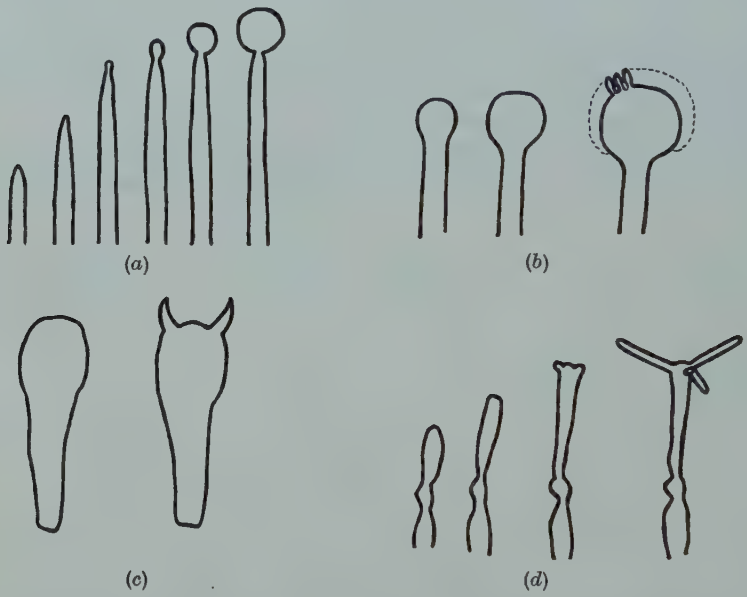

Fig. 3. Examples of fungi in which the arrestment-swelling-branching mechanism may operate in the production of fruiting structures. (*a*) Phycomyces sporangiophore (redrawn from Castle, 1942). (*b*) The developing conidiophore of Aspergillus. (*c*) The young basidium (redrawn from Corner, 1948). (*d*) The conidium of *Heliscus longibrachiatus* Ingold (redrawn from Ingold, 1942).

If the interpretation of the experimental results and its application to the shape of conidiophore branch systems in the Hyphomycetes is valid, it not only reduces the apparently complex range of conidiophore forms to simple variations on one theme but also raises other problems of organization and control. It is, for example, implicit in the interpretation given above that the process of 'wall-setting' is independent of the general extension of the hypha and one simple explanation of events leading to the arrestment of the primary conidiophore hypha, in nature, would be in an alteration in the relative rates of extension and 'wall-setting' such that setting overtakes extension and arrests the hypha. But unless this alteration of relative rates is large one might expect the hypha to taper before stopping. Such a sudden drop in extension rate relative to wall-setting might, however, arise from the sudden fall below a threshold value of one of the substances needed by the apex for extension. That this threshold may be in some way connected with the vertical transport of materials in the erect hypha or with external gradients, for example that of humidity, from the substrate, might be deduced from the narrow limits of variation in height and branch form shown by the fungus under one set of environmental conditions.

Such speculations, insecurely based as they are, nevertheless, indicate the sort of mechanism through which nuclear control and its interaction with the environment may work, in this particular group, and they are a stimulus to further experimental work.

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Periodicity of growth in Rhacomitrium lanuginosum. By J. H. Tallis. Department of Botany, University College of Wales, Aberystwyth[1]

(With 7 Text-figures)

The remarks I am about to make refer nominally only to a single moss species, *Rhacomitrium lanuginosum* (Hedw.) Brid., but they can be taken as applying in part probably to most mosses. However, certain features of growth are seen at their simplest in *Rhacomitrium*, and an uncritical extension of the conclusions reached to other mosses must be undertaken with care.

R. lanuginosum consists basically of an elongated main stem and rather numerous short lateral branches, and these latter typically show an aggregation together into definite branch zones arranged at regular intervals along the main stem By periodic measurement and observation it can be shown that one branch zone only is formed each year, and that the annual growth is from 5 to 15 mm. per year. Maximum growth occurs in the spring and summer, and a period of elongation growth of the main stem in March, April and May is followed closely by lateral branch initiation and development in late May, June and July; further slight elongation growth of the main stem occurs in early autumn. The actual numbers of lateral branches in each branch zone, and also the extent to which they elongate, vary with environmental factors. Thus at high altitudes, in a cold and humid climate, there are only two or three very short laterals in each zone, whereas at sea level, in a drier warmer climate, there may be up to a dozen variously elongated laterals per zone. The development of lateral branches in nature may be caused by a combination of high light intensity and an alteration of drying and humid conditions,

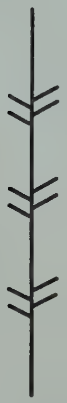

Fig. 1

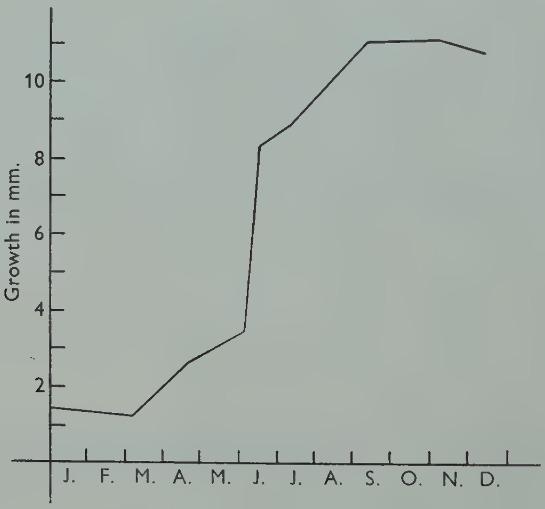

Fig. 2

Fig. 1. Diagrammatic stem of *Rhacomitrium lanuginosum* to show the zonation of the lateral branches.

Fig. 2. Growth curve (elongation growth only) for *Rhacomitrium lanuginosum* at 750 m. in North Wales for 1956. The dry spring of this year rather delayed the commencement of growth, which normally occurs in March, and similarly the very wet August prolonged elongation growth beyond the normal. (Reproduced by courtesy of the *Journal of Ecology*.)

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[1] Now at the University of Manchester.

perhaps with the mean temperature above a certain threshold value, of about 12–14° C. This is suggested chiefly by a comparison of the growth curve with the relevant climatic data. In culture (which is difficult, and has so far been possible only for relatively short periods) under humid shaded conditions, the initiation of lateral branches can be delayed by up to 4 weeks, but apparently not indefinitely. When the stem apex is removed, and the lateral branch next below takes over the function of the main stem (giving sympodial growth), or when regeneration occurs from stem fragments, lateral branches are not formed until after 2–3 years' elongation growth has taken place. However, where, under certain favourable conditions, elongation of certain of the lateral branches occurs in nature in the year subsequent to initiation, lateral branches are formed on these as on the main stem. These results would suggest, perhaps, some active principle formed at the main apex and affecting growth at the proximate lateral apices. In other mosses (e.g. *Eurhynchium striatum* (Hedw.) Schp. emend Størmer) it appears from field observations that high humidity and shading may completely suppress lateral branch formation for up to a year.

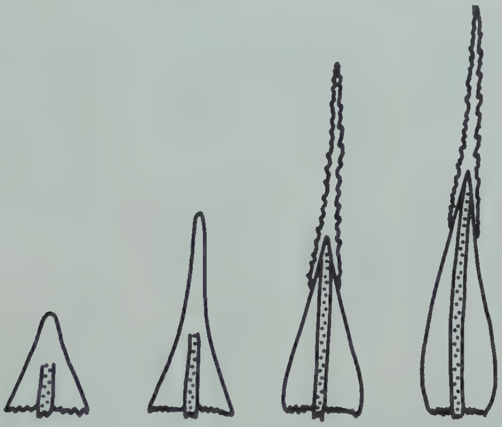

Fig. 3. Progressively maturing leaves of *Rhacomitrium lanuginosum*, showing the precocious development of the hair-point.

The leaf of *R. languinosum* consists of a longly triangular green lamina terminating in a hyaline hair-point which may be nearly as long as the lamina. The hair-point is formed early in leaf development, and reaches maturity while the lamina is still relatively small. Hence it should reflect fairly closely the conditions at the growing apex. If leaves are removed at regular short intervals along the main stem and the lengths of the hair-points measured, a cyclical fluctuation in length of the hair-point is found to occur: the peaks occur consistently in the lateral branch zones, whilst leaves along the inter-zone portions of the main stem have rather short hair-points. A similar cyclic fluctuation has been claimed for the length of the green lamina, but I have not as yet been able to confirm this. However, a cyclical fluctuation of lamina length or of the length/breadth ratio does occur in other mosses. As with the lateral branches, length of the hair-point is determined both by internal and by external factors. I am using these two words in a very loose sense, and in the ultimate analysis they may well be found to be inseparable. Light and humidity are probably the most important external factors, but it is difficult to separate their effects: thus plants grown in shade or in very humid conditions have hair-points shortened to 50 % of normal or rarely even almost entirely wanting. In the summer of 1956 in North Wales at high altitudes (when the weather was consistently cold, wet, and dull), hair-points formed during that period were reduced to 65 % of normal. However, only rarely do external factors reduce the length of the hair-point to values similar to those at the minima of the cyclic fluctuations. Removal of the stem apex followed by sympodial regeneration results in the formation of leaves with hair-points very short or absent, and normal hair-points are formed only after an interval of 2–3 years. Short lengths of stem (*ca.* 2 cm. long) with the apex intact and cultured on moistened filter-paper show normal monopodial growth, but successively formed leaves show a progressive reduction in the length of the hair-point—e.g. relative lengths along one such newly formed stem were 84, 80, 75, 65, 36, 19, 15, 17. Actual depletion of some active principle appears to be involved here.

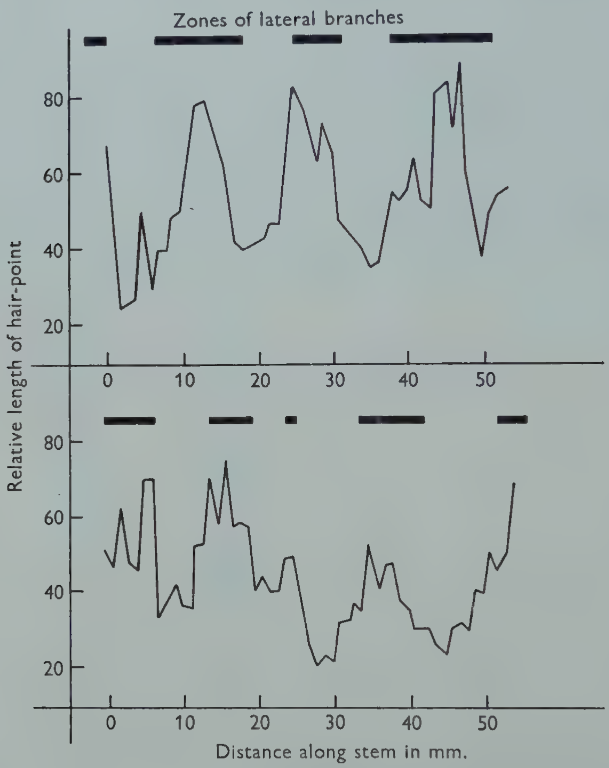

Fig. 4. The lengths of hair-points of leaves of *Rhacomitrium lanuginosum* removed at 1 mm. intervals along the main stem.

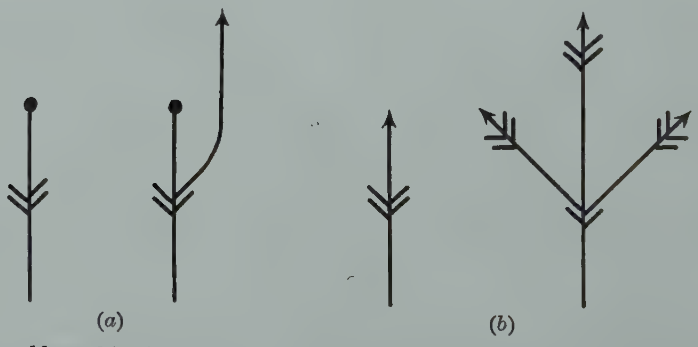

Fig. 5. Growth and branching in *Rhacomitrium lanuginosum* (diagrammatic). (*a*) Main apex removed: no laterals formed in first year. (*b*) Persistent main apex: laterals formed in first year.

Thus both stem and leaf show a closely linked annual rhythm, which can be modified by external factors to some extent; however, there is in addition an underlying internal control (with the proviso mentioned above) associated apparently with a substance or substances produced at the stem apex and passing into the newly formed lateral branches; this substance appears to be produced chiefly when elongation growth of the main stem is slow, but when conditions for assimilation are favourable (maximum assimilation occurs experimentally at 12–15° C.), and its presence results in lateral branch formation and well-developed hair-points to the leaves. Alternatively, these effects could be associated with the *absence* of a substance which is produced only during active elongation growth under relatively unfavourable conditions. The evidence so far does not permit of a definite conclusion either way.

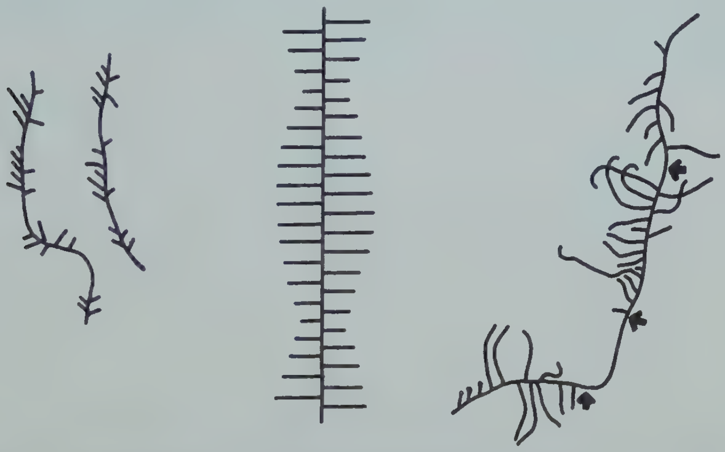

Fig. 6. Growth types in pleurocarpous mosses. On the left two stems of *Hypnum cupressiforme* Hedw. var. *ericetorum* B. & S. to show zonation of lateral branches; in the centre, portion of the stem of *Hylocomium splendens* (Hedw.) B. & S. to show regular arrangement of lateral branches of differing lengths; and on the right, one stem of *Rhytidiadelphus triquetrus* (Hedw.) Warnst. showing 'irregularly' arranged laterals. The arrows indicate the presumed positions of successive annual increments; the lack of lateral branches along one increment is the result of submergence of the stem during this period below other stems.

A similar annual rhythm, affecting stem or leaf or both, probably occurs in most mosses. This phenomenon of periodicity is well known in acrocarpous mosses from the studies of Hagerup (1935), Lackner (1939), and Jendralski (1955). Here apical growth is terminated by the formation of sex organs, and growth is contained by a branch arising a short distance below the apex. Even when sex organs are not formed, annual increments can generally be recognized by seasonal differences in the size and shape of leaves. Periodicity has been less studied in pleurocarpous mosses, where the sex organs develop on lateral branches and where, consequently, any rhythms are shown chiefly in the disposition and length of the lateral branches. The definite zonation of laterals seen in *R. lanuginosum* occurs in several other mosses (though in a less distinct form) such as *Hypnum cupressiforme* Hedw., *Acrocladium cuspidatum* (Hedw.) Lindb. and *Camptothecium lutescens* (Hedw.) Brid. Several pleurocarpous mosses have lateral branches regularly arranged along the whole length of the main stem, but typically these laterals are of differing lengths, such that each annual increment has an approximately elliptical outline. *Hylocomium splendens* (Hedw.) B. & S. and *Cratoneuron commutatum* (Hedw.) Roth are good examples. Again, several pleurocarpous mosses, such as *Rhytidiadelphus*, appear to have an irregular distribution of laterals along the main stem; however, usually it can be shown that the distribution of the laterals is not statistically random, but that definite cycles occur characterized by different densities (and often also lengths) of the lateral branches. Even in such unpromising material as *Sphagnum*, quite definite annual increments can usually be recognized.

Whatever the distribution of lateral branches it appears fairly general among pleurocarpous mosses that maximum elongation growth of the main stem and active lateral branch development do not occur concomittantly. Perhaps four types of growth in mosses can be recognized, though this subdivision is as yet very tentative.

(1) The *Rhacomitrium* type, where lateral branches are both initiated and develop at one season of the year only.

(2) The *Hylocomium splendens* type, where it appears that there are alternating periods of elongation growth and lateral branch growth throughout the year; in the phases of elongation growth lateral branch rudiments are initiated, but generally they do not develop until elongation growth has slowed down, or until the rudiments are a certain distance back from the apex.

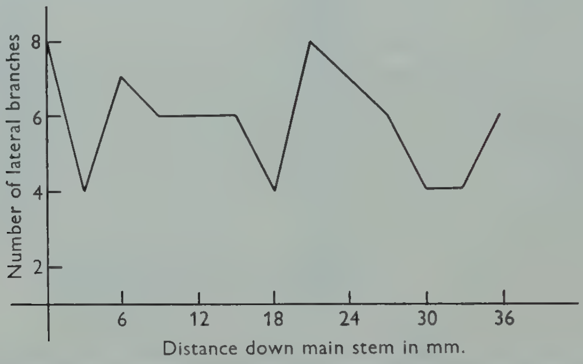

Fig. 7. Distribution of fascicles (clusters of lateral branches) along the main stem of *Sphagnum fuscum* (Schp.) Klinggr. The data are given as the numbers of fascicles in successive 3 mm. portions of the main stem.

(3) The *Rhytidiadelphus* type, intermediate between the previous two, with the laterals not initiated at regular intervals throughout the year, but more abundantly at one particular season. This is probably the commonest type in pleurocarpous mosses.

(4) The *Sphagnum* type, where lateral branches are apparently initiated at regular intervals at the apex, but subsequently become non-regular due to differential elongation of the main stem.

This classification, it must be emphasized, is only tentative, and may require modification when the annual growth cycles of more mosses have been studied in detail.

Sometimes these lateral branch rhythms are accompanied by corresponding rhythms in size or shape of leaves; however, often it appears that, while there may be a basic underlying rhythm, environmental modifications of this rhythm may be so considerable as almost to obscure it.

To sum up, there are perhaps three major questions raised by these results:

(1) To what extent is the initiation of lateral branches controlled by internal factors and to what extent by external factors?

(2) What factors govern the balance between growth of the main axis and of the lateral branches?

(3) What factors govern the elongation in subsequent seasons of some only of the lateral branches?

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Effects of certain cultivation treatments on the morphology of some British species of Drepanocladus. By E. Lodge, Royal Holloway College, University of London

(With 7 Text-figures and Table 1)

Drepanocladus fluitans (Hedw.) Warnst. and *D. exannulatus* (B. & S.) Warnst. are two closely related but well-defined aquatic species which occur commonly in Britain. Like many aquatic mosses, each exhibits a wide range of form, though the variation shown by one does not overlap with that shown by the other. In spite of their relative abundance, these species rarely produce sex organs under natural conditions, so that it seems likely that many of the plants composing them will be of clonal origin. They therefore provide very suitable material for use in an investigation of the effects of certain environmental factors on morphological variation.

A morphological analysis of these two species will be described in detail elsewhere (for a preliminary report see Lodge, 1958). It will suffice to say here that some of the more interesting points to emerge from this analysis concerned the structure and arrangement of the cells in the basal angles of the leaves of the two species. In *D. fluitans*, these cells are different in structure from the other cells of the lamina and form minute auricles. An examination of a wide range of British material of this species showed that two quite distinct types of angular cells occurred. These, which for convenience have been called type A and type B, are illustrated in Fig. 1. The angular cells of type A were thin walled, slightly inflated and arranged in three to four tiers extending from the leaf margins to the nerve. Those of type B, on the other hand, were pigmented, rectangular in outline, with appreciably thickened, frequently pitted walls, arranged in a single row adjacent to the nerve, but in two to three rows at the margins. All the leaves of any one shoot of this species were found to have angles which were uniform in appearance, and usually all the shoots examined from any one gathering had identical angles.

In *D. exannulatus* the angular cells form more prominent auricles. Once again, however, an analysis of a wide range of material of this species revealed the existence of two distinct types of angular cells. These, are illustrated in Fig. 2. Again, for convenience the two types have been called A and B. In this species the angular cells of type A were large, thin walled and strongly inflated, arranged in two to three tiers extending from the margins of the leaf to the nerve, forming conspicuous auricles. Those of type B however, were large, elongated and inflated, usually with pigmented appreciably thickened walls, arranged in a single row extending from the margins of the leaf to the nerve, forming auricles less conspicuous than those of type A. As in *D. fluitans*, the shape and arrangement of the angular cells was constant for all the leaves of any one shoot.

EFFECT OF THE ENVIRONMENT ON THE MORPHOLOGY OF *DREPANOCLADUS FLUITANS* AND *DREPANOCLADUS EXANNULATUS*

Effects of submergence on leaf shape

A sample of *D. fluitans* with narrowly lanceolate leaves having angular cells of type A, was collected from a pool and divided into three sections which were subsequently treated in the following way:

(1) Dried and preserved as a herbarium specimen.
(2) Grown submerged in an aquarium.
(3) Grown on moist peat.

The living material was allowed to grow in a greenhouse for about 3 months before measurements were made of the length of the nerve and the total length of the leaf.

Fifty leaves were taken from the submerged sample and fifty leaves from the non-submerged sample, in each case five leaves being taken from ten individual shoots of the moss. Measurements of nerve length and leaf length were also made on twenty leaves from a single shoot of the herbarium specimen.

The relation between the length of the leaf and the length of the nerve after these three treatments is shown in Fig. 3. A camera lucida drawing of a single leaf from each of the cultivated portions of the clone has been included in the figure for the purposes of comparison.

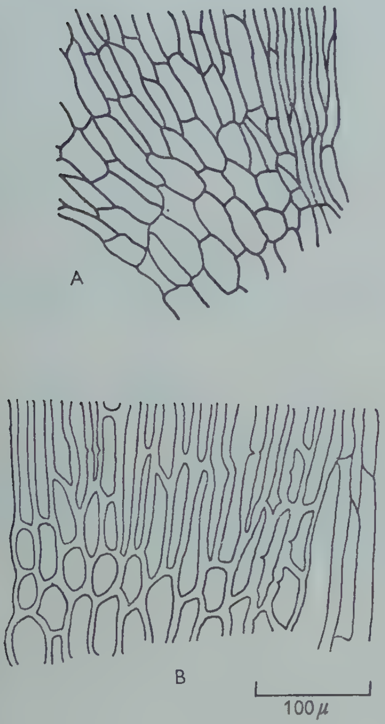

Fig. 1

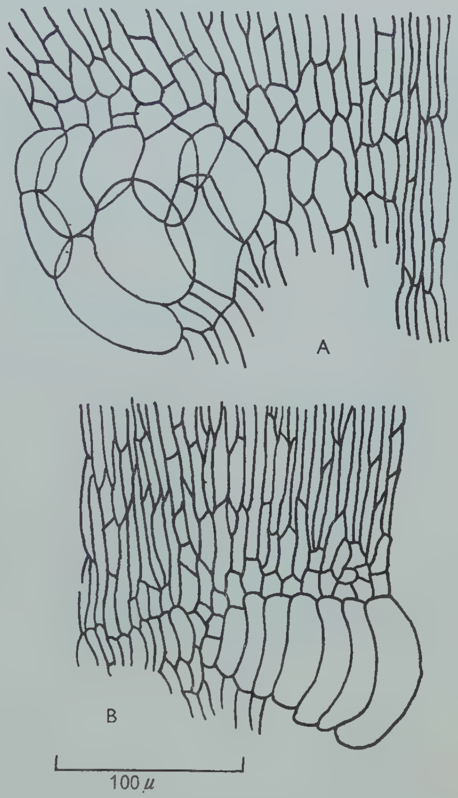

Fig. 2

Fig. 1. *Drepanocladus fluitans*. The two types of angles. A, type A; B, type B.

Fig. 2. *Drepanocladus exannulatus*. The two types of angles. A, type A; B, type B.

This experiment shows conclusively that plants with narrowly lanceolate leaves can be induced to produce ovate-lanceolate leaves when treated in an appropriate manner. Clearly, the production of shorter and wider leaves in this case can only be associated with growth in air. It is not merely due to growth in the greenhouse, since the control plant, grown in the greenhouse under submerged conditions, still gave rise to leaves which were long. It is interesting to note the correlation between nerve length and leaf length in all three portions of the clone, which indicates that there can be no very marked decrease in the length of the nerve, relative to the length of the leaf, in growth in air.

The experiment was repeated, using material of *D. exannulatus* with angular cells of type A, which before collection had been growing submerged. The relation between the length and width of the leaf after the three treatments is shown in Fig. 4. Again, camera lucida drawings of individual leaves from each of the cultivated sections of the clone have been included in the figure for the purposes of comparison.

These data indicate that plants of *D. exannulatus* can also be induced to produce leaves of different shape on cultivation under different conditions. Leaves which develop under conditions of submergence are considerably longer and in this case slightly wider than leaves which are produced in air. This species is extremely distinct in its morphological response to these environmental conditions, as the amount of variation in leaf

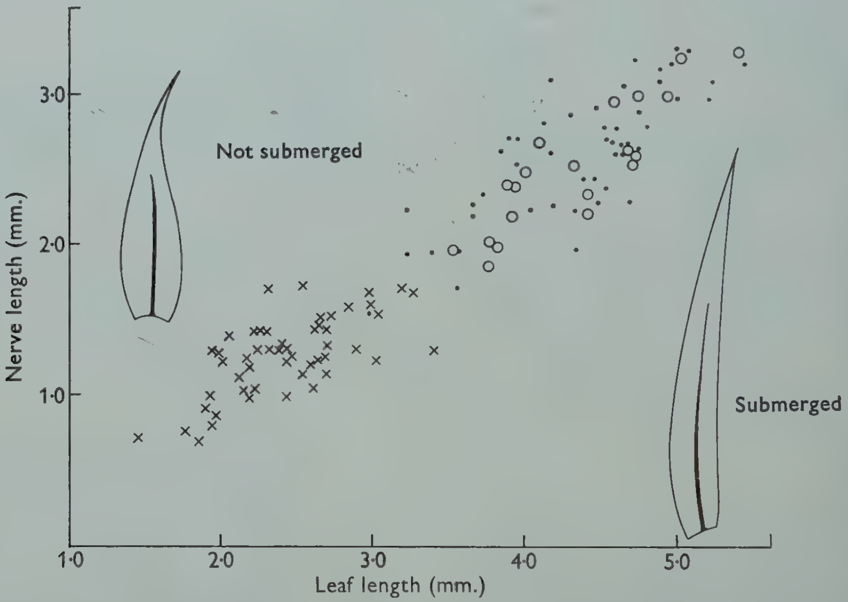

Fig. 3. *D. fluitans*. The relation between the length of the leaf and the length of the nerve after various cultivation treatments. ○, leaves from herbarium specimen; ●, leaves from submerged part of clone; ×, leaves from the portion of the clone grown on peat.

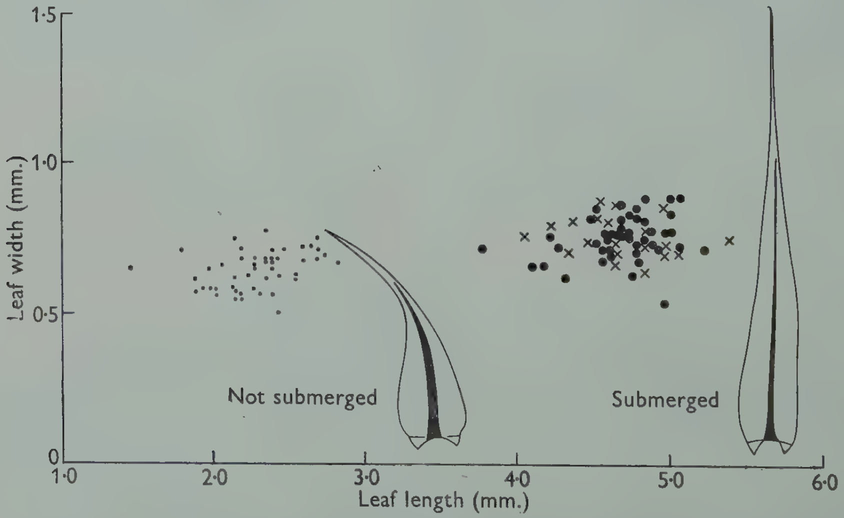

Fig. 4. *D. exannulatus*. Relation of leaf length to leaf width after various cultivation treatments. ×, leaves from herbarium specimen; ●, leaves from submerged part of clone; •, leaves from the portion of the clone grown on peat.

length and leaf width in the differently treated samples is relatively small. Fig. 4 also shows that there is no significant difference between the shape of leaves produced under submerged conditions in the field and those produced under submerged conditions in the greenhouse.

In order to determine whether there was any difference in the length of the nerve relative to the length of the leaf between the two cultivated portions of the clone, the ratio of these two lengths has been calculated for each leaf measured. These data are grouped into the histograms presented in Fig. 5; submerged and non-submerged plants have been treated separately. The two histograms, though clearly overlapping, have quite distinct peaks, suggesting that the nerve length of the submerged plants is slightly longer, relative to the length of the leaf than that of plants grown on peat. A statistical test showed that the difference in the mean value of the two groups is indicative of a real difference between the parent sources. In addition to causing an increase in the length of the leaf of *D. exannulatus*, therefore, submergence also causes an increase in the length of the nerve, though under the conditions of this experiment, the extent of this increase in nerve length is small.

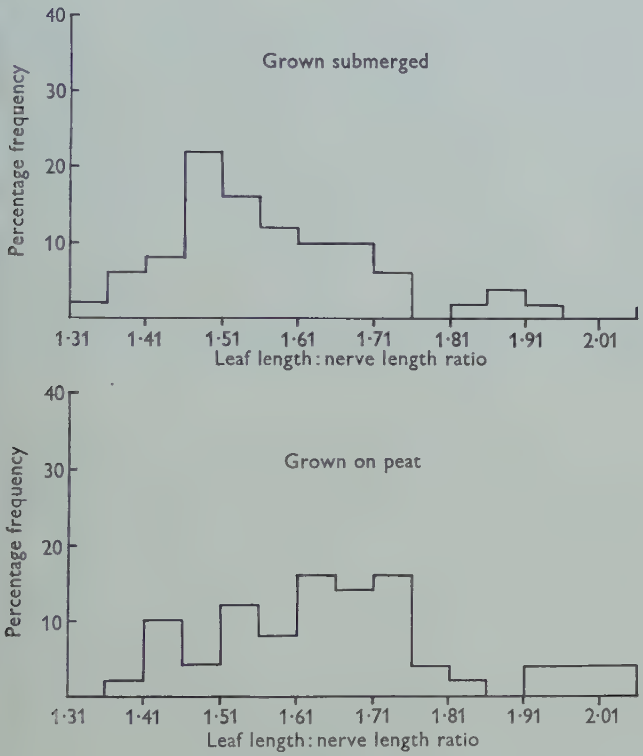

Fig. 5

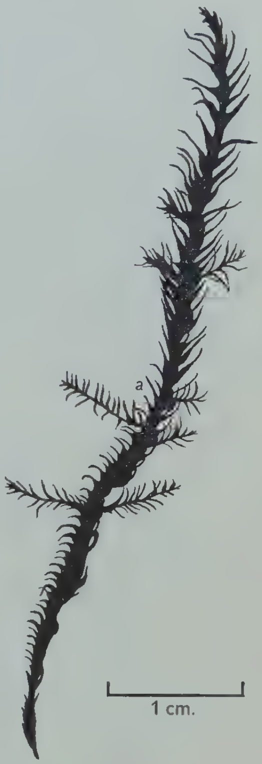

Fig. 6

Fig. 5. *D. exannulatus.* Distribution of leaf length to nerve length ratio classes in samples which have been grown either submerged or non-submerged.

Fig. 6. *D. fluitans.* Single shoot from a clone which has been grown submerged. *a* represents the point of demarcation between the growth of the main shoot before and after experimental treatment. All lateral branches produced during the experiment.

Growth of material of *D. fluitans* and *D. exannulatus* under the conditions described above did not bring about a change in the type of angular cells; young leaves developed during cultivation had angles identical to those of leaves developed before the treatments were applied.

Fig. 6, which is a drawing of a single shoot of *D. fluitans*, grown submerged under greenhouse conditions, shows other morphological effects of submergence. The original material was unbranched with strongly falcate, ovate-lanceolate, closely inserted leaves. Submergence has caused an increase in the length of the internode, the production of lateral branches, and the formation of straight leaves instead of falcate leaves.

EFFECTS OF THE CHEMICAL COMPOSITION OF THE CULTURE SOLUTION ON THE LENGTH OF THE LAMINA CELLS

A series of ten culture solutions were made up according to the schedule of Voth & Hamner (1940), so that although the total concentration of each solution was different from that of the others, individual ions were always present in the same proportions. A large number of individual shoots were separated from a single clone of *D. fluitans*, and from these, 120 shoots were selected for uniformity in size and appearance. Batches of twelve of these shoots were grown for 3 months in each of the ten concentrations of solution, in otherwise uniform conditions. At the end of this period of growth, the shoots were removed and subjected to a morphological examination. The experiment was repeated using material from other sources.

Salt concentration appeared to have no effect on the shape of the leaves or on the structure of the angular cells. It did, however, have a marked effect on the length of the cells of the leaf and this is illustrated in Fig. 7, where the mean length of cell is plotted against the relative concentration of each solution.

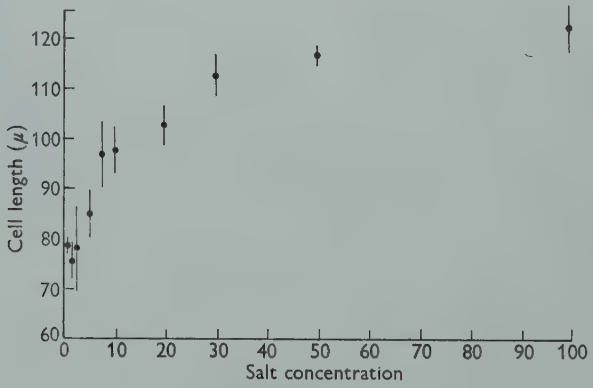

Fig. 7. *D. fluitans.* Relation of mean lamina cell length and relative salt concentration of the medium.

From this figure it is apparent that over most of the range of salt concentrations used, there is an increase in cell length with increase in salt concentration. In the lower part of the range of salt concentrations, however, i.e. in solutions with a salt content of less than 10 % of that of the most concentrated solution, salt concentration appears to have no significant effect on cell length. It is in water of this concentration that the moss is found in nature.

The experiment was repeated using more dilute solutions. Growth occurred in all concentrations, but decreased in amount as the solution became more dilute. Morphological examination of the plants showed, however, that over this range salt concentration had no effect on leaf cell length.

Plants of *D. exannulatus* subjected to exactly the same treatments showed a similar relationship between salt concentration and lamina cell length. As with *D. fluitans*, however, the salt concentrations effective in causing an increase in cell length are considerably greater than those of the pools and flushes in which the species is found in nature.

EFFECTS OF LIGHT INTENSITY ON THE INTERNODE LENGTH OF *DREPANOCLADUS FLUITANS*

Measurements of the length of the internode were made on a few populations of *D. fluitans*, originally collected from non-submerged habitats, after they had been grown on moist peat for 2 years in the greenhouse. During this time, each plant received approximately 75 % of full daylight.

Table 1. *Mean internode length of individual shoots of* Drepanocladus fluitans *grown under different intensities of illumination*

Type of angular cells	Specimen no.	(Average length of the internode (mm.)) Plants grown in field	Plants grown in 75 % illumination	Plants grown in 35 % illumination
A	249·54	0·431	0·464	0·494
	19·55	0·391	0·402	0·477
	50·55	0·324	0·342	0·375
B	219·54	0·544	0·593	0·637
	252·54	0·525	0·550	0·642
	174·55	0·382	0·399	0·472

These measurements were compared with the results of a similar survey of internode lengths made on herbarium material prepared at the time the cultivated material was originally collected. The data obtained are given in Table 1, and it can be seen that in the case of each population, growth in the greenhouse resulted in an appreciably longer internode. In order to determine whether this increase in internode length had been brought about by the decrease in illumination which resulted from growth in the greenhouse, the pots containing these populations were shaded, so that each now received approximately 35 % of full daylight. After 3 months of growth under these conditions, the average length of the internode was redetermined in the newly produced parts of the stem. These measurements, which are also given in Table 1 show that a further increase in internode length had occurred. It is clear from these results, that the length of the internode is greatly influenced by the amount of light which the plant receives.

It has previously been noted that growth in submerged conditions also brings about an increase in internode length, and this may be indirectly due to a decrease in illumination brought about by light absorption in the liquid. In this connexion, however, it appears that although growth in air under conditions of reduced illumination caused a slight overall decrease in leaf dimensions, the leaves were approximately the same shape as those of the herbarium specimens, presumably grown in conditions of greater light intensity in the field. This indicates that the change in shape of the leaves of this species, in growth in submerged conditions, cannot be attributed to a decrease in illumination.

THE IMPLICATIONS OF THE EXPERIMENTS

The experiments show conclusively that within the two species, form is largely influenced by the environment. One morphological character, however, which is not altered by growth in different conditions, is the structure and arrangement of the angular cells. An examination of a wide range of British material has revealed that *D. fluitans* (Hedw.) Warnst. and *D. exannulatus* (B. & S.) Warnst. are composed of two groups of plants each characterized by a distinctive pattern of angular cells. These groups must clearly represent distinct genotypes and deserve taxonomic recognition as such.

The experiments also show that the morphological responses of the four genotypes to similar changes of environmental factors are almost identical. As might be expected in aquatic organisms, submergence has an important effect on form, causing an alteration in the shape and arrangement of the leaves of all four genotypes, and in the length of the nerve of the two which constitute *D. exannulatus*. Leaf arrangement is also influenced by the intensity of the illumination which the plant receives. In addition to their intrinsic interest, these findings have important taxonomic implications, since morphological characters such as leaf shape, cell length and nerve length, have been used by many systematists to delimit taxa of infra-specific rank, within each of these two species.

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Changes in leaf arrangement in individual fern apices.

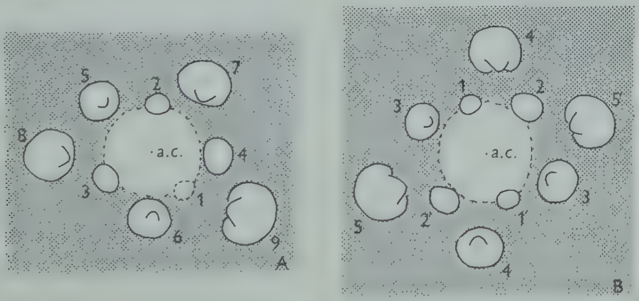
By Elizabeth G. Cutter and Bruce R. Voeller,[1] Department of Botany, University of Manchester

(With Plates **8** and **9** and 5 Text-figures)

Introduction

The orderly and characteristic arrangement of organs, usually leaves or branches, is a very general phenomenon throughout the Plant Kingdom. Indeed, the various different arrangements, or phyllotactic systems, that are recognized may occur in different major groups of plants. The very ubiquity of these arrangements suggests that the underlying mechanism, and its explanation, must be of a very general kind. Yet leaf arrangement in ferns, for example, has often been considered as a special case, because the leaf primordia are widely spaced on the apex and are not in contact, as they are in the majority of flowering plants. Richards, however, has pointed out that theories of phyllotaxis must be applicable not only to flowering plants but also to the ferns: 'The fern presents a simpler picture of the essential phyllotaxis phenomena than does the flowering plant, yet it has been regarded just as an aberrant type which must be accommodated, by the use of subsidiary hypotheses, to theories elaborated from the contemplation of a more specialized system; the converse attitude would seem to provide a safer approach' (Richards, 1948, pp. 241–2).

Both Richards (1948) and Wardlaw (1949*a*) consider that leaf arrangement in ferns provides support for a 'field theory' of phyllotaxis, rather than for one based on spatial considerations, involving the contact of visible primordia or zones around them which are unavailable for other primordia. These views are, however, contested by Snow & Snow (1952), who adhere to the theory that new primordia arise in 'the first available space' (Snow & Snow, 1931). They consider this view to be supported by a considerable body of experimental evidence.



Text-fig. 1. (A) Surface view of the apex with spiral phyllotaxis shown in Pl. **8**, fig. 1. *a.c.*, apical cell. × 14. (B) Surface view of the apex with bijugate phyllotaxis shown in Pl. **8**, fig. 2. × 14.

By means of many experimental treatments it has now been shown that the phyllotaxis of a plant can be greatly modified. For example, apices with spiral phyllotaxis have been obtained from the two halves of diagonally split apices of decussate species (Snow & Snow, 1935; Snow, 1942); in species with spiral phyllotaxis, the direction of the 'genetic spiral' has been reversed by various experimental treatments, both in flowering plants and ferns (Snow & Snow, 1931, 1933; Wardlaw, 1949*b*). As Richards (1948, p. 219) concludes: 'These results demonstrate conclusively that the phyllotaxis of an apex is dependent on circumstances and, if interfered with, may readily change from one system to another.'

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[1] Present address: Rockefeller Institute, East 66th Street and York Avenue, New York 21, N.Y., U.S.A.

The observations now presented are of some importance in a general consideration of phyllotaxis because they demonstrate the following: (i) the occurrence of several different phyllotactic systems in a species in which there is no contact between leaf primordia; (ii) changes from one system to another in apices not subjected to surgical treatment; and (iii) the possibility of relating such changes to the general growth of the apex. The relevant observations are still very incomplete, but they indicate the potentialities of further studies along these lines.

The fern used in this investigation was *Dryopteris aristata* (Vill.) Druce (*D. austriaca* (Jacq.) Woynar). While the majority of specimens of this fern have Fibonacci spiral phyllotaxis (Pl. **8**, fig. 1 and Text-fig. 1A), a small proportion (some 8·6 %) are bijugate (Voeller & Cutter, 1959). In bijugate specimens leaf primordia occur in opposite pairs, each pair diverging from the preceding pair by an angle corresponding to half the Fibonacci angle (Pl. **8**, fig. 2 and Text-fig. 1B). Two genetic spirals, each passing through one member of each pair of leaves, can be constructed (Bravais & Bravais, 1837; Church, 1904; Snow, 1951). The average divergence angle along each spiral in these bijugate ferns was 70½°.

MATERIALS AND METHODS

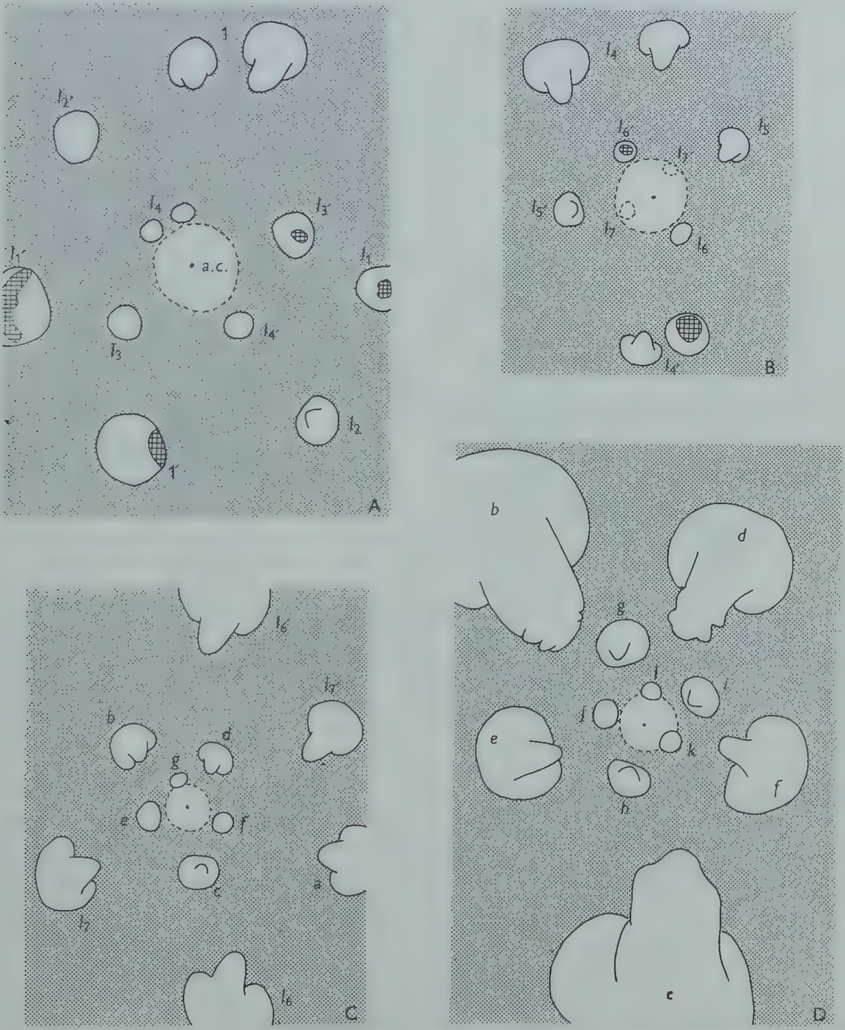
The shoot apices and young leaf primordia of rhizome tips of *D. aristata* were exposed to view by removing older leaves and scales, and the plugs of tissue (about 3½ × 2½ × 2½ cm.) maintained in the laboratory in pans of damp peat (Wardlaw, 1944, 1947). Since bijugate specimens were only occasionally obtained, a collection of such apices was built up over a period of a few months. Subsequently, some of these apices were surgically treated; the others were simply maintained in the pans of peat and observed occasionally under a binocular microscope. Between observations, scales were allowed to grow on the subapical regions, and the outer leaf primordia were allowed to expand into small leaves. In the thirteen apices which were surgically treated, the majority of visible leaf primordia were punctured with a steel sewing needle, as follows: in four apices, the paired P_1 primordia were left intact, older primordia being destroyed; in five specimens, one P_1 primordium was left intact; and in the remaining four apices all visible primordia were obliterated. The phyllotaxis of the new primordia was then observed. This experiment was similar to that earlier carried out by R. Snow (1951) on apices of seedlings of the bijugate species *Dipsacus laciniatus* L.

Drawings of apices as seen in plan were made at intervals under a binocular microscope, using a camera lucida, the following conventions being observed: the approximate outline of the apical cone is indicated with a broken line, the subapical region being stippled; in bijugate apices the members of a pair of primordia are labelled 1 and 1′, successively older pairs being 2, 2′; 3, 3′; 4, 4′, etc.; where the phyllotaxis is spiral, successive primordia are labelled 1, 2, 3, 4, etc. Primordia which were invisible at the beginning of the experiment, but which have developed during its course, are called I_1, I_2, I_3, etc., I_1 being the first to appear (Snow & Snow, 1931). In successive drawings of the same apex taken over a period of time, the orientation of the specimen is the same; in apices subjected to experimental treatment, primordia which were formed in bijugate sequence are labelled I_1, I_1'; I_2, I_2', etc., as above, but primordia formed subsequently which were not in a bijugate arrangement are assigned letters of the alphabet, either in the order of their formation, or where this was not known exactly, on the basis of size. In those apices which were not experimentally treated, and were only observed periodically, the primordia have been renumbered in successive drawings.

After fixing in chrom-acetic acid, the apices were embedded in paraffin wax and sectioned transversely at a thickness of 10–20 μ. The sections were stained in safranin and Delafield's haematoxylin.

OBSERVATIONS AND RESULTS

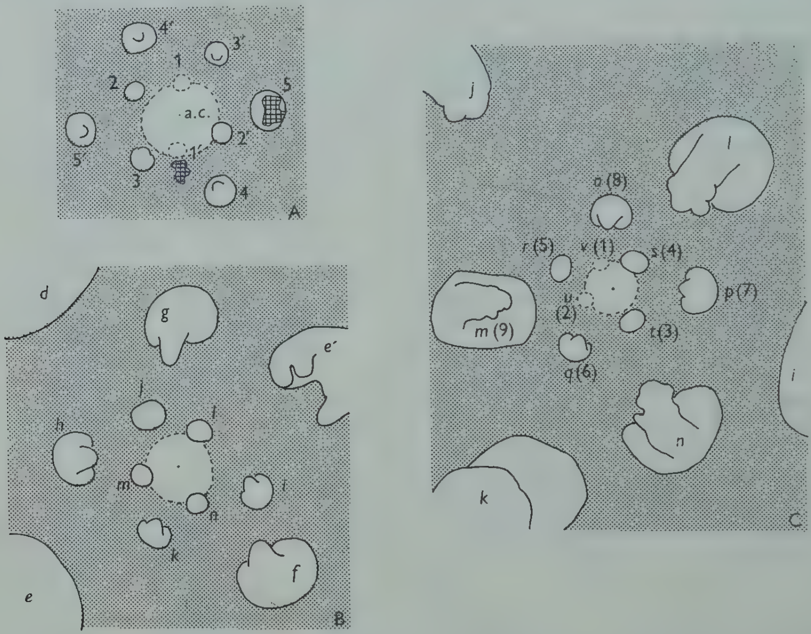
In the majority of specimens in which the leaf primordia had been destroyed by puncturing, the primordia which were subsequently formed were arranged in a bijugate system, at least for several weeks. In some instances, the angle between successive pairs of primordia was rather variable, and occasionally exceeded 90°, thus sometimes reversing the direction of the two genetic spirals. After comparable experiments on *D. laciniatus*, R. Snow (1951) found an increase in divergence angle which was maintained for several plastochrones, the angle sometimes exceeding 90°. For comparative purposes, therefore, angular measurements were made from successive camera lucida drawings of surface views of *Dryopteris* apices; they are likely to be less accurate than Snow's measurements, which were taken from transverse sections. The angles measured were those



Text-fig. 2. Expt. 2, in which all visible primordia except the paired P_1's were damaged. (A) 4 weeks after the experiment. The angle of divergence has increased, until the arrangement of I_2–I_4 is nearly decussate. (B) 4 weeks later. Paired I_6's and I_7's have now been formed. (C) 12 weeks after the experiment. After the primordium *a*, which might possibly have been part of a double I_7', the leaf arrangement is spiral. (D) 4 weeks later. Five more primordia have been formed, in spiral sequence. All ×14.

between the lines joining the centres of successive pairs of leaf primordia, whether or not these passed across the centre of the shoot apex. Where double leaf primordia occurred—and these were not infrequent—the line was drawn between the two primordia occupying the site.

Although individual divergence angles were variable, successive angles did increase to some extent and the mean angle of divergence in individual specimens after the experiment was sometimes, but not always, greater than it had been previously. Occasionally, as in Snow's (1951) experiments, the phyllotaxis became nearly decussate (Text-fig. 2 A), and indeed, several angles greater than 90° occurred. In general, therefore, the preliminary results of this experiment were comparable with those of Snow (1951) on *Dipsacus*.



Text-fig. 3. Expt. 8, in which all visible primordia were punctured. (A) 2 days before the experiment was carried out. (B) 12 weeks after the experiment. The six youngest leaf primordia are apparently arranged approximately in trimerous whorls. (C) 16 weeks after the experiment. The phyllotaxis is now spiral, of the accessory series 1, 3, 4, 7, 11, ..., with a mean divergence angle of 100°. Numbers in parentheses after the letters indicate the sequence of the primordia along the spiral. All × 14.

Subsequent observations, however, revealed a change in the phyllotaxis of the majority of these specimens. In many, the leaf arrangement became spiral, usually of the Fibonacci series 1, 2, 3, 5, 8,... (Text-fig. 2C, D), but occasionally belonging to the accessory series 1, 3, 4, 7, 11,... (Text-fig. 3C); in a few, the arrangement of the primordia approximated to whorls of three. The latter type of phyllotaxis consisted of whorls of three primordia which were of approximately, but not exactly, equal size; these primordia were not always quite equally spaced, nor at exactly equal radial distances from the centre of the apex, but alternated with the members of the next whorl, members of each whorl being, in consequence, diametrically opposite to members of the preceding and subsequent whorls (Text-fig. 4D). This arrangement might be more accurately described as 'pseudo-whorled'. In Table 1 the phyllotactic changes which occurred in bijugate specimens in which leaf primordia had been punctured are summarized. Since Richards (1951) has pointed out that the transverse phyllotaxis system is completely defined by the angle of divergence and the phyllotaxis index, and that the latter affords a measure for the comparison of different phyllotactic systems, the mean angle of divergence and the phyllotaxis index (P.I.) of the specimens at various times are given in Table 1 wherever possible.

Since these changes had not occurred until some considerable time (8–16 weeks) after the leaf primordia had been punctured, it seemed unlikely that they could be directly attributed to the original experimental treatment. Accordingly, bijugate apices which had been maintained in pans of peat in the laboratory for some 7 months, and which had been left undisturbed for 3 months, were then examined. Comparable changes in leaf arrangement were found to have taken place in these specimens also (Table 2). It therefore appears that these phyllotactic changes were not a direct result of the experimental puncturing of visible leaf primordia. In Table 2 it can also be seen that the direction of the twin genetic spirals in the bijugate specimens was not necessarily retained when they became spiral.

Table 1. *Changes in leaf arrangement in bijugate apices in which the majority of visible primordia had been punctured*

Expt. no.	P.I. at time of expt.	Primordia left undamaged	Time after beginning of expt. (weeks)	Phyllotaxis	Mean divergence angle (°)	Phyllotaxis index (P.I.)
1	3·68	Both P_1's	12	Uncertain (apex damaged)	—	—
2	3·59	Both P_1's	4	Approx. decussate	—	*ca.* 2·99
			12–16	Spiral	137·25	2·75
7	2·81	Both P_1's	18	Bijugate	70	—
			23	Spiral	*ca.* 136	*ca.* 1·97
10	2·91	Both P_1's	8–12	Spiral	140·8	2·13
5	3·88	One P_1	8–12	Trimerous whorls	—	2·89
6	3·64	One P_1	12	?	—	—
			16–18	Spiral	136·6	2·58
9	3·48	One P_1	12	Bijugate	*ca.* 70	3·13
			16	?	—	—
12	3·23	One P_1	12–16	? Spiral (reversed) or pseudo-whorled	137·5 (variable)	2·52
			23	Spiral	139	2·72
13	3·02	One P_1	12–16	Spiral	136·7	2·48
3	3·49	None	12	Spiral	139	2·82
4	3·95	None	12	Spiral	136	2·70
			16	Pseudo-whorled	—	—
8	3·19	None	12	Trimerous whorls	—	2·99
			16	Spiral (3 + 4)	100	3·02
11	3·50	None	12	Trimerous whorls	—	2·74
			16	Spiral	140	2·63

In some instances it was possible to observe the transition from one system of phyllotaxis to another. Examples of such transitional stages are illustrated in Text-figs. 4 and 5. In some specimens the increase in divergence angle described above resulted ultimately in a nearly decussate arrangement, and this was followed by inequality of one of the pairs of primordia. The members of this pair were of unequal size, presumably not having been formed simultaneously, and were often not quite opposite. The next primordium was then usually, but not always, formed in the larger gap and nearer to the older primordium of the pair; a spiral system was thereby initiated (Text-fig. 5C).

Occasionally, however, the failure of a pair of primordia to be formed simultaneously, and in opposite positions, led instead to the inception of a system of trimerous whorls, or pseudo-whorls. This can be seen in the fifth experiment, in which all visible primordia except one P_1 had been punctured. Paired I_1's, I_2's and I_3's were formed in an approximately bijugate arrangement; the I_4's, however, were formed at an angle which just reversed the spirals, and one of them was a double primordium (Text-fig. 4B). One I_5 (*b*) was formed before the other (*c*), and two other primordia (*c*′ and *c*″) were formed at approximately the same time as the latter (Text-fig. 4C). These three primordia formed a pseudo-whorl, and subsequent primordia were formed in alternating pseudo-whorls (Text-fig. 4D), thus establishing the system. In an untreated bijugate apex (C) which became spiral, of the series 1, 3, 4, 7, 11,..., a paired leaf arrangement became established again, possibly as a result of damage to the youngest primordium. The average angle of divergence was 79° (Table 2), and the system may be considered to be bijugate. Members of a pair were not quite equal at inception, however, and this difference became accentuated during subsequent growth.[1]

Table 2. *Changes in leaf arrangement in bijugate apices maintained in the laboratory without surgical treatment*

Specimen	Initial phyllotaxis index	Time after the first observation* (months)	Phyllotaxis†	Mean divergence angle (°)	Phyllotaxis index
A	3·71	4	Bijugate (L)	70	2·72
		7	Spiral (L)	137·6	2·46
		8	Spiral (L)	139	2·25
B	3·64	4	Bijugate (R)	73	2·65
		7	Spiral (L) (transition)	141	2·09
		8	? Spiral (L)	148·4	2·03
C	3·26	4	Bijugate (L)	65	3·03
		7	Spiral (R) (3+4)	101·7	2·59
		8–10	Bijugate (R)	79	—
D	3·0	4	?	—	—
		7	Spiral (L)	136·3	2·42
		8	Spiral (L)	139·3	2·34
E	—	4½	Bijugate (L)	69	2·95
		7	Approx. decussate	80‡	2·40
		8	Spiral (R) (transition)	139	2·41
F	3·95	4½	Spiral (R) or pseudo-whorled	137 (variable)	2·82
		7	? Spiral (R) (irreg.)	142·3 (variable)	2·35
		8	Spiral (R)	140	2·28

* This is taken as the date of the first set of drawings, about 2 months after collection of the apices.
† The direction of the genetic spiral(s) is indicated as right (R) or left (L).
‡ Successive angles rising: 74°, 81° and 85°.

Serial transverse sections of the specimens served to confirm the external observations. Selected sections of specimen *E*, illustrated in Text-fig. 5, are shown in Pl. **9**, figs. 1–5. The transition from bijugy to a Fibonacci spiral system is well demonstrated in these sections. Pl. **9**, fig. 6 shows a transverse section of an experimental specimen which became first spiral and then pseudo-whorled. At the level of the section illustrated, the oldest whorl of three primordia is just joining the axis, older primordia being spirally arranged.

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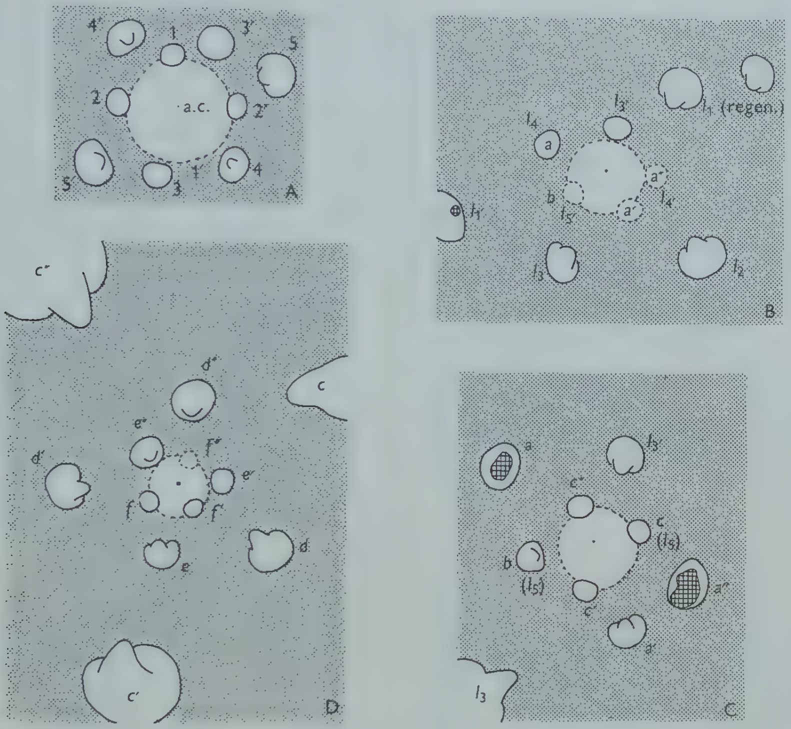
[1] *Note added in proof.* 12–13 months after the first observation, specimen C had become spiral, of the Fibonacci series 1, 2, 3, 5, 8,....

In the majority of specimens distinctive systems of phyllotaxis were displayed, but in a few the type of leaf arrangement was somewhat more indeterminate; likewise the transitional stages were more puzzling. Space does not permit further discussion of these apices at present.



Text-fig. 4. Expt. 5, in which one P_1 was left undamaged. (A) 2 days before the experiment. Only one of the paired P_1 primordia is visible. (B) 6 weeks later. Primordia I_1–I_4 have been formed in bijugate sequence; I_4' is a double primordium. One I_5 (*b*) has also been formed. (C) 8 weeks after the experiment. The other I_5 (*c*) has been formed, together with two other primordia (*c*′ and *c*″). These three primordia constitute a pseudo-whorl. (D) 12 weeks after the experiment. The leaf primordia are arranged approximately in trimerous whorls. All ×14.

Discussion

In initially bijugate apices of the fern *Dryopteris aristata*, maintained under laboratory conditions, three distinct and easily recognizable systems of phyllotaxis (four if the approximately decussate system be included) developed, with no experimental treatment other than the removal of the outer leaves and periodic removal of scales, etc. Of these various systems, only bijugate and spiral (of the Fibonacci series 1, 2, 3, 5, 8, . . .) have ever been recorded in the very large number of apices of *D. aristata* collected from natural habitats. Since spiral apices of this species, maintained under similar conditions, retained their spiral leaf arrangement for periods of up to 12 months (Cutter, 1955), it appears that bijugy is less stable than spiral phyllotaxis in this species.

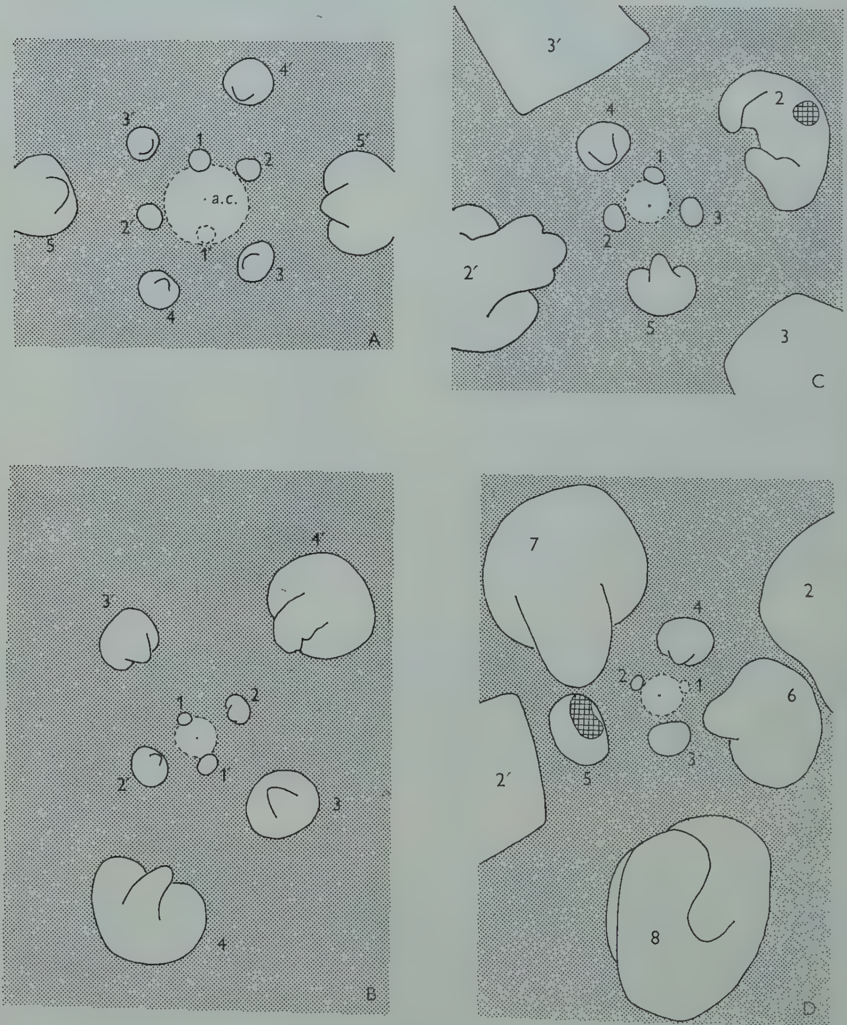
Specimens belonging to the accessory series 1, 3, 4, 7, 11, . . ., having a divergence angle of 99·5°, are reported to occur occasionally in plants which normally exhibit the Fibonacci angle (Richards, 1948). It is of particular interest that Church (1904, p. 198) reported that examples of higher members of this series ‘occur in *Dipsacus* and *Helianthus*, side by side with bijugate representatives...’.

Thus, the present findings are that:

(i) four distinct types of phyllotactic system (spiral (1, 2, 3, 5, 8,...); spiral (1, 3, 4, 7, 11,...); bijugate; and trimerous pseudo-whorls) can occur in a species in which the leaves are not in contact at their inception, and consequently that such contact is not an essential condition for the initiation or maintenance of these systems;

(ii) these systems are, at least to some extent, interchangeable; and therefore

(iii) the establishment of these systems is not controlled by spiral or whorl-forming ‘tendencies’ of a direct hereditary nature (see also Voeller & Cutter, 1959).



Text-fig. 5. Specimen E, maintained in the laboratory without surgical treatment. (A) $4\frac{1}{2}$ months after the first observation. The phyllotaxis is still bijugate. (B) 7 months after the first observation. The angle of divergence has increased, so that the phyllotaxis is nearly decussate. Note that primordia 1 and 1′ are not of equal size. (C) 8 months after the first observation. Primordia 1–5 are in spiral sequence, older primordia paired. Primordia 4 and 5 represent 1 and 1′ of Fig. B, primordia 2, 2′ and 3, 3′ of that drawing being so numbered again. (D) 3 weeks later. Three more primordia have been formed in spiral sequence. P_4 represents P_1 of Fig. C. *See also* Pl. **9**, figs. 1–5. All ×14.

It is important to seek some explanation for the observed developments in *Dryopteris*, and to consider to what extent it may be applicable to other groups of plants.

These changes in leaf arrangement may have resulted either from slight random fluctuations in growth, or from more considerable changes in the various components of apical growth. Some of the phyllotactic systems observed were themselves not stable for long, but more general trends were also evident. For example, it may be noted that the changes from bijugy towards decussation, and from approximately decussate to spiral phyllotaxis which have been described in the fern *D. aristata*, are apparently not uncommon in flowering plants. Thus Snow (1954) has reported that in specimens of the bijugate species *Dipsacus sylvestris* which are approaching flowering, the angles between the last four pairs of foliage leaves are significantly greater than the mean divergence angle found in the seedling rosettes. Also, a transition to spiral leaf arrangement often occurs in decussate species at the approach to flowering (Snow & Snow, 1935). Thus this general trend, from bijugy through decussation or near-decussation to a spiral arrangement, occurs in both ferns and flowering plants. It seems likely that there is a general explanation which is applicable to both groups, and that it is unlikely to be based on leaf contacts.

Richards (1948) has suggested that bijugy might be derived from an opposite decussate arrangement by a fall in plastochrone ratio, the position of a pair of incipient primordia then being influenced by the two preceding pairs, instead of one pair only. Snow (1951) subsequently carried out experiments designed to test this suggestion on seedlings of the bijugate species *D. laciniatus*. He removed the leaves of these plants as far as the P_1's, or only to the P_2's or P_3's, and observed the effect on the subsequent phyllotaxis. His expectation was that, if Richards's hypothesis were correct, removal of the P_1's should result in an increase of the angle I_1–I_2 to 90°, removal of young P_2's should similarly affect the angle P_1–I_1, and removal of P_3's should have no effect; and that the angle between later pairs of leaf primordia would revert to approximately 72·7°, the normal angle for the species. In fact, he found that the divergence angles between successive pairs of leaves continued to increase for five or six plastochrones after the experiment, some angles being greater than 90° and reversing the twin genetic spirals. Four specimens differed from the rest, however; of these, one became spiral and one formed whorls of three. Snow considered that his findings, particularly those angles which reversed the spirals, were difficult to reconcile with Richards's suggestion. 'So the inhibition hypothesis does not account for the angles later than I–I_2 after removal of P_1's, nor later than P_1–I_1 after removal of P_2's, nor for any of the increases after removal of P_3's. The reversed angles are not only unexplained on the inhibition hypothesis, but contrary to it.' (Snow, 1951, p. 301.) Snow, who was concerned mainly with the reasons for the divergence of bijugy from decussation, suggested an explanation for his observations which comprised two factors. The first factor was concerned with the contacts of the leaf primordia with older primordia or their united rims; the second was the pressure resulting from the contact of the vertical parts of the paired P_2's with the shoot apex in *Dipsacus*.

Snow (1951, p. 309) himself pointed out that '. . . many more observations are needed to establish how generally either or both of the factors suggested may be at work in causing bijugy', and considered it possible that in other species bijugy might be caused by physiological inhibitions. It has now been shown that some specimens of *Dryopteris aristata* have bijugate phyllotaxis, and that when experimental treatment as nearly comparable to that of Snow (1951) as possible was carried out on such specimens results rather similar to those in *Dipsacus* were obtained, initially at least. Yet in *Dryopteris* the leaf primordia are not in contact, nor do their vertical parts touch the apical cone. Thus although comparable results have been obtained in a flowering plant and in a fern, it is unlikely that the explanation suggested by Snow (1951) for the former can apply to the latter, and an alternative interpretation must be sought.

Phyllotaxis may be more narrowly viewed as a succession of comparatively unrelated divergence angles. But it may also be considered as a coherent system or arrangement—the view which the present writers consider to be the more appropriate—in which case any disturbance of the growth of an apex, such as must have resulted from the present experiments and those of Snow (1951), may be expected to have an effect on leaf arrangement of more than momentary duration. Thus not one divergence angle, but several, may be affected; and this in turn may influence the subsequent arrangement. If this is conceded, both the observations of Snow (1951) and those now reported seem, in the main, to be explicable in terms of a field theory of phyllotaxis. This type of theory has sometimes been termed a 'repulsion theory' (Snow & Snow, 1947, 1948, 1952). Such a term suggests that the effect of existing leaf primordia on the position of new ones is due wholly to the emission of inhibitory, or repelling, substances: as envisaged by the present writers the 'field effect' of a leaf primordium may comprise both competition for substances necessary for growth and the emission of inhibitory ones. It seems important to emphasize this rather broad concept of a field effect. Snow (1951), for example, considers that removal of the P_2's in *Dipsacus* will have obliterated any inhibitory effect that they may have on the I_1's, so long as the latter are not determined; if, however, competition for substances essential for growth constitutes one element of this possible inhibitory effect, it seems possible that the P_2's may have already exerted at least some part of their effect prior to their removal (they ranged in length from 0·25 to 0·9 mm. during the plastochrone (Snow, 1951, p. 296)). Also, it is possible that the angles greater than 90° which reversed the genetic spirals may be less incomprehensible than Snow believed when considered in relation to the growth of the whole apex.

In terms of a field theory, if two or more leaf primordia are formed simultaneously they will occur at the maximum tangential distance from each other, i.e. at 180° if there are two of them. The next pair of primordia will occur at right angles to these (assuming the absence of other fields). If enough growth has occurred, so that the first pair of primordia is at a sufficient radial and vertical distance for its field effect to be negligible, the third pair of leaf primordia will be formed above the first, giving a decussate system. If, however, rather less radial or vertical growth has occurred during the plastochrone, the oldest pair of leaf primordia will deflect the incipient pair, and bijugy may result, in the manner suggested by Richards (1948). If we now consider the converse argument, it may be seen that in a bijugate apex greater vertical growth during the plastochrone would lead to a lessening of the effect on a pair of incipient primordia of the fields of the pair of leaves two plastochrones older, thus tending towards a decussate arrangement. Snow's (1951) experiments—involving the destruction of a number of pairs of leaf primordia in seedling plants—may well have altered the balance of the various components of apical growth. The conditions under which the apices of *Dryopteris* were maintained also might well lead to a similar change.

The majority of the bijugate specimens of *Dryopteris* eventually became spiral. One of Snow's (1951) treated specimens of *Dipsacus* became spiral at the outset; it is conceivable that others might have done so also had the periods of treatment and observation been longer, though since bijugy is the normal leaf arrangement in this species it may well be more stable than it is in *Dryopteris*. In terms of a field theory, this change in leaf arrangement could result from a lengthening of the time between the formation of the individual primordia of a pair, theoretically nil but in fact sometimes appreciable in bijugate apices of *Dryopteris* kept under laboratory conditions (unpublished observations). As a consequence, the members of a pair become unequal, and are situated at different radial and vertical distances from the centre of the apex; thus they exert differential effects on the next primordium, or pair of primordia (Text-fig. 5).

The occurrence, and possible origin, of bijugate specimens in *D. aristata* will be discussed elsewhere. Apart from a brief description of the transition in one specimen from bijugy to trimerous pseudo-whorls, no attempt has been made in this paper to account for this latter type of phyllotaxis. It may be recalled, however, that one specimen of

Dipsacus laciniatus, in which leaf primordia down to the P_1's inclusive had been removed, also formed whorls of three leaves (Snow, 1951). Snow considers that there is evidence of an active whorl-forming process in *Dipsacus*, similar to that which he earlier postulated in the Labiatae and considered to comprise one factor for equalizing the levels of the leaf primordia and another for equalizing their lateral spacing (Snow, 1942). As Snow (1951) himself concedes, the factor which equalizes the lateral (tangential) spacing of the members of a whorl could be a physiological inhibition; however, the factor which leads to the formation of two or more leaf primordia at the same level—the 'whorl-forming tendency' of Snow—still remains unexplained at present.

Richards (1948) has explained theoretically how various systems of phyllotaxis may be derived. The present observations seem to provide some practical support for his views, and to indicate a possible means of acquiring further information along similar lines. Richards (1948) suggested that bijugy was derived from a decussate arrangement by a fall in plastochrone ratio (this being equivalent to a rise in phyllotaxis index (Richards, 1951)). From tables 1 and 2 it can be seen that the converse change, starting from bijugy and tending towards decussation and thence to spiral arrangements, was indeed accompanied by a fall in phyllotaxis index in individual apices of *Dryopteris*, as would be expected on Richards's hypothesis. This progressive fall in phyllotaxis index will not be discussed here, since further studies on phyllotaxis in relation to apical growth are in progress.

SUMMARY

In thirteen apices of *Dryopteris aristata* with bijugate phyllotaxis, the majority of the visible leaf primordia were destroyed by puncturing, and the specimens maintained under observation in the laboratory. New primordia were at first formed in a bijugate arrangement, but there was a tendency for the angles of divergence to increase. Subsequently, the phyllotaxis became spiral or pseudo-whorled. Other bijugate apices kept in the laboratory without surgical treatment, and observed periodically during a period of 8 months, displayed similar changes in leaf arrangement. Thus four different systems of phyllotaxis—spiral, of the Fibonacci series 1, 2, 3, 5, 8,...; spiral, of the accessory series 1, 3, 4, 7, 11, ...; bijugate; and trimerous pseudo-whorls—were observed in a species in which the leaf primordia are not in contact. The significance of this is discussed, and an attempt is made to examine the causes of transition from one system of phyllotaxis to another.

These observations are compared with those of Snow (1951) after similar experiments on seedling plants of the bijugate species *Dipsacus laciniatus*. It is concluded that the results of the two sets of experiments are comparable, at least initially, and that therefore any explanation of them, and of bijugy itself, should be applicable to both ferns and flowering plants, and is most likely to be found in a field theory of phyllotaxis.

ACKNOWLEDGEMENT

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EXPLANATION OF PLATES

Plate 8

Surface views of apices of *Dryopteris aristata* after removal of the outer leaves and scales.

Fig. 1. Apex with spiral phyllotaxis. $P_1 - P_9$ present. The direction of the genetic spiral is clockwise. *See* Text-fig. 1A. × 40.

Fig. 2. Apex with bijugate phyllotaxis. Five pairs of leaf primordia are present. The direction of the genetic spirals is anticlockwise. *See* Text-fig. 1B. × 40.

Plate 9

Figs. 1–5. Basipetal transverse sections of specimen E, which was originally bijugate but became spiral after 8 months in the laboratory without surgical treatment. *See* Text-fig. 5D for labelling, etc.

Fig. 1. At the insertion of P_1 (right) on the apex. P_1–P_8 are present, P_1–P_7 being in spiral sequence, P_7 and P_8 nearly opposite. × 30.

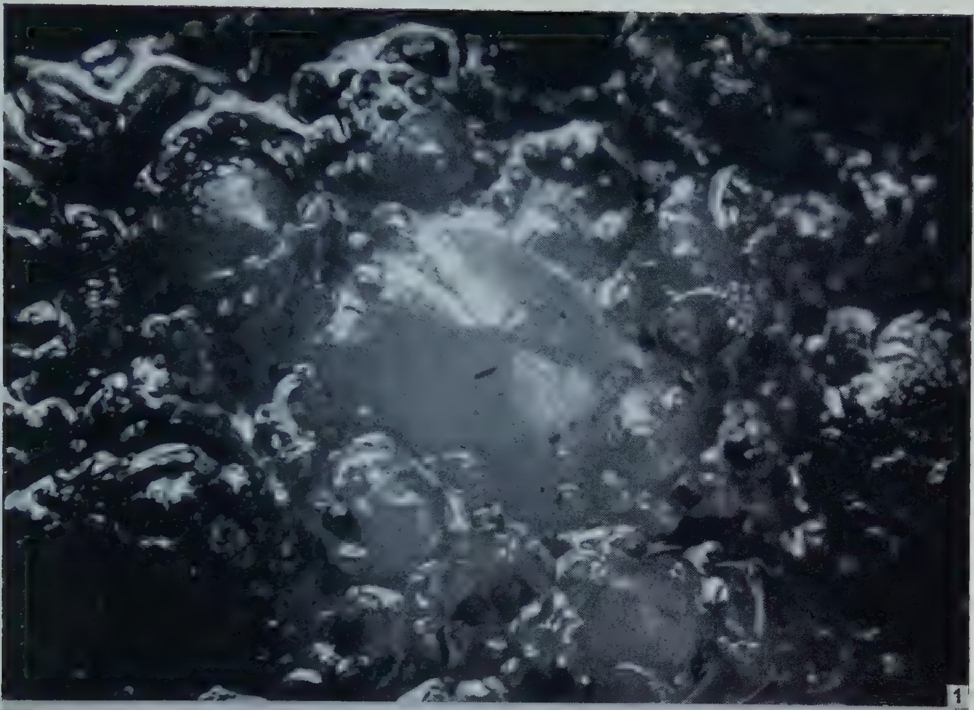
Fig. 2. 70μ lower down. P_1–P_4 have joined the apex. Other primordia as in Fig. 1. × 30.

Fig. 3. At the insertion of P_7 and P_8 on the axis. Another pair of primordia (left and right) are also visible. 220μ below Fig. 2. × 10.

Fig. 4. At the insertion of the pair of primordia visible in Fig. 3. The bijugate arrangement of the leaf primordia is now clear. × 5.

Fig. 5. 2925μ below Fig. 4. Several pairs of leaf primordia in a bijugate arrangement are evident. × 5.

Fig. 6. Transverse section of Exp. 4. This apex was originally bijugate, but became first spiral and then pseudo-whorled. In this section the older leaf primordia are spirally arranged, but the three primordia just joining the axis are in a pseudo-whorl. × 10.



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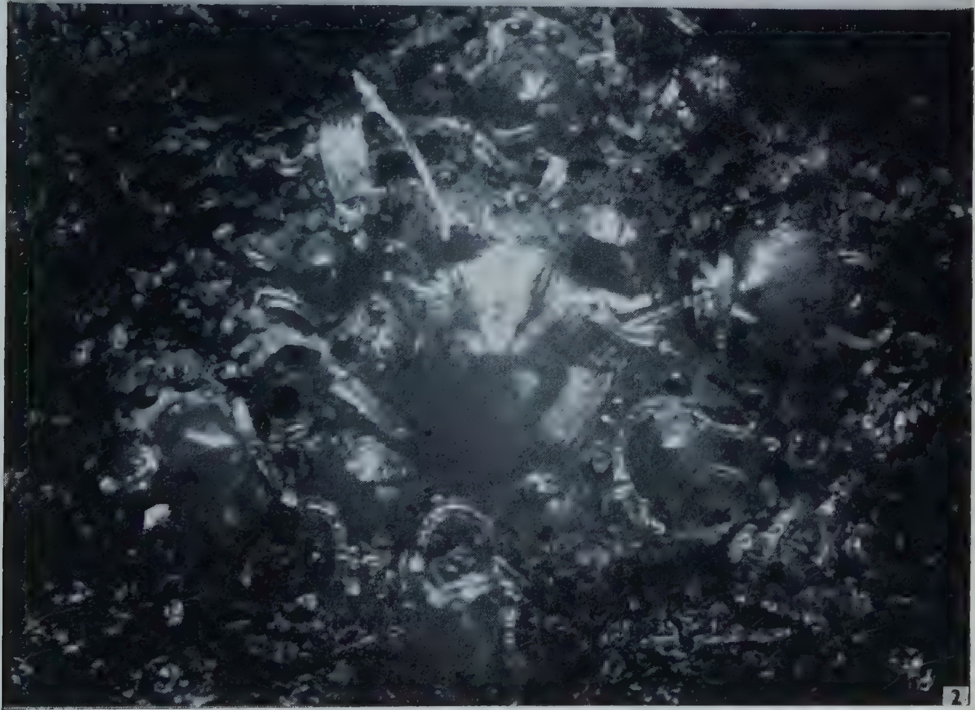

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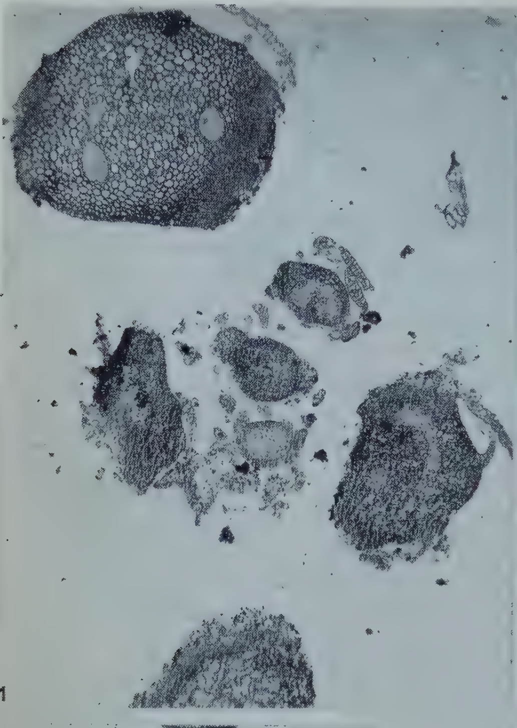
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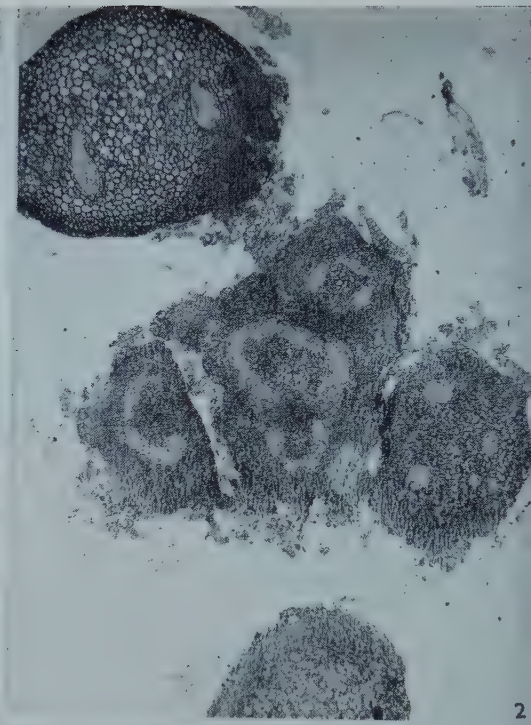
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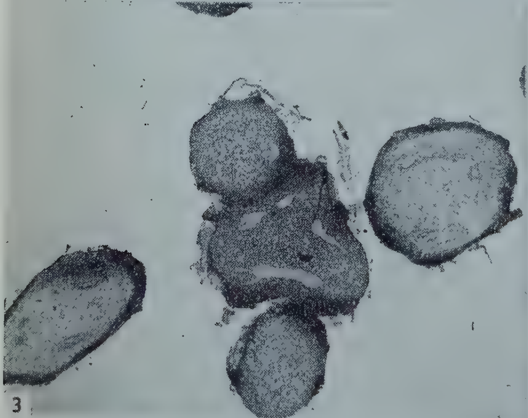
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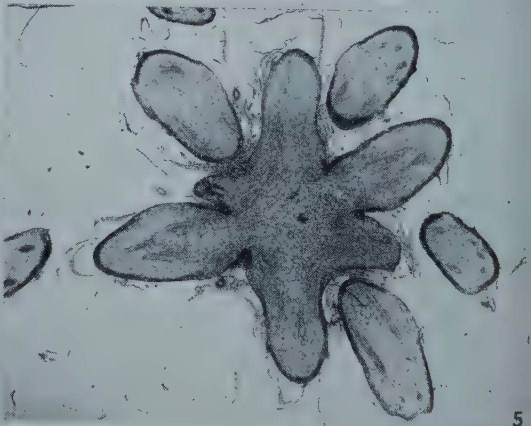
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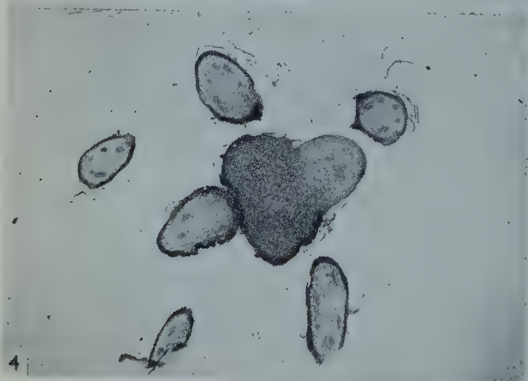
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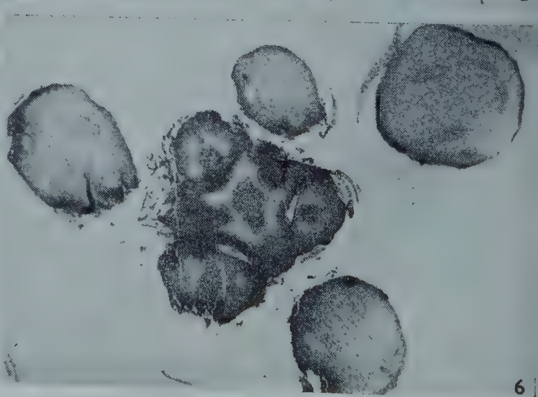
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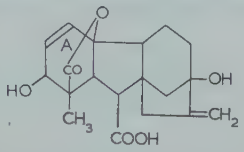
Morphogenetic effects of the gibberellins.

By P. W. Brian, Akers Research Laboratories, Imperial Chemical Industries Ltd., Welwyn, Hertfordshire

Introduction

The discovery of the gibberellins dates from 1926. While investigating a disease of rice caused by *Gibberella fujikuroi* (Saw.) Wr. [imperfect state *Fusarium moniliforme* Sheld.], a characteristic symptom of which is lengthening of stems and leaves of infected plants, Kurosawa (1926) found that the treatment of rice seedlings with cell-free filtrates from cultures of the fungus would induce these same abnormal growth symptoms. Yabuta & Hayashi (1939*a*) isolated small quantities of a highly active crystalline material from such culture filtrates. They called this 'gibberellin A' and proposed for it the molecular formula $C_{22}H_{26}O_7$. In an unsuccessful attempt to prepare this substance, Curtis & Cross (1954) isolated instead a pure compound, with similar physiological activity, but clearly distinct chemically from 'gibberellin A'. They called this new substance gibberellic acid $C_{19}H_{22}O_6$) and it has since (Cross, Grove, MacMillan, Moffatt, Mulholland, Seaton & Sheppard, 1959) been shown to have the following structure:



Three other pure gibberellins have since been isolated, viz. gibberellin A_1 ($C_{19}H_{24}O_6$), a dihydro derivative of gibberellic acid in which the double bond in ring A is reduced (Takahashi *et al.* 1957*a*; Grove, Jeffs & Mullholland, 1958); gibberellin A_2 ($C_{19}H_{26}O_6$) (Takahashi *et al.* 1957*a*) and gibberellin A_4 ($C_{18}H_{22}O_5$ or $C_{19}H_{24}O_5$) (Takahashi *et al.* 1957*b*). The nature of the original 'gibberellin A' is obscure; Japanese workers have recently concluded that it was a mixture, but we cannot now be sure which of the known pure gibberellins it contained. Gibberellins A_1, A_2 and A_4, and gibberellic acid, seem to have qualitatively similar physiological activity, though gibberellic acid is most active (Bukovac & Wittwer, 1958). Because of this similarity, in the rest of this paper the precise compound or mixture used in experimental work is not usually specified, the more general term *gibberellin* being in many ways more convenient.

As is shown later a characteristic feature of the gibberellins is that they induce abnormally great extension of shoot structures of many plant species when applied exogenously, but the response is greatest from genetic dwarfs. They also induce flowering of many biennials and long-day plants kept in non-inductive conditions of photoperiod and temperature. The significance of these observations has been much increased by the discovery of 'gibberellin-like' substances in many plant tissues, that is substances capable of inducing physiological responses of the kind just mentioned. Such responses cannot in general be elicited by application of indolylacetic acid or other natural auxins. 'Gibberellin-like' substances have been found in shoots and roots of peas, in many seeds, in inflorescences of *Brassica* and in coconut milk (Bünsow, Penner & Harder, 1958; Lang, Sandoval & Bedri, 1957; Lona, 1957; McComb & Carr, 1958; Murakami, 1957; Phinney, West, Ritzel & Neely, 1957; Radley, 1956, 1958; Radley & Dear, 1958; West & Phinney, 1956). The 'gibberellin-like' substance demonstrated in seeds of runner-beans (*Phaseolus multiflorus* Willd.) by Radley (1958) has been isolated by MacMillan & Suter (1958) and shown to be gibberellin A_1. Gibberellin A_1 has also been found in seeds of french bean (*P. vulgaris* L.) (West & Murashige, 1958). Thus the gibberellins, or at least some of them, are natural plant hormones, which we must in future consider in any discussion of control of morphogenesis in plants.

In this paper I propose to describe some of the effects of exogenously applied gibberellin on the development of plants, and then to discuss the significance of these observations in the light of the discovery that the gibberellins are natural plant hormones. I shall not attempt to cover the whole rapidly expanding literature; more complete bibliographies will be found in the reviews of Stowe & Yamaki (1957) and Brian (1959).

Since I have drawn most of my examples from recently published work, I may appear to underestimate the Japanese work published between the discovery of growth-promoting activity in culture filtrates of *Gibberella fujikuroi* in 1926 and the awakening of interest outside Japan some 4 or 5 years ago. I should like to dispel any such impression immediately. The isolation of 'gibberellin A', the demonstration that it affected growth of most plants, and the description of the general nature of its effects on shoot and root growth were primarily Japanese contributions to our knowledge and it is regrettable that their work received so little attention in other countries for so long.

STEM GROWTH

(*a*) *Day-neutral herbaceous plants*

In non-branching plants the most striking effect of gibberellin treatment is increase in internode length without any great increase in internode number; this is exemplified by the response of the garden pea. In branching plants, for example, Cupid sweet pea or dwarf bean (*Phaseolus vulgaris*), the internode extension is increased but in addition branching is inhibited and the main axis continues to elongate so that a higher proportion of the internodes formed are to be found in the main axis. The general habit of the plant is thus markedly changed. The increase in internode length is due to a more rapid extension; the time during which extension of any one internode takes place is in fact slightly reduced, thus the more rapid extension results in longer internodes in spite of more rapid ageing of the cells (Brian & Hemming, 1955; Brian, Hemming & Lowe, 1958, 1959).

Though application of gibberellin usually enhances apical dominance when applied to intact plants, it does not always do so and branching may actually be encouraged, for example, in Pinto bean (Gray, 1957). Gibberellin does not directly inhibit lateral buds as indolylacetic acid does (Kato, 1953); neither does it directly encourage development of normally inhibited lateral buds (Wickson & Thimann, 1958). It appears that it prolongs the activity of apical buds if applied while they are still active, thus enhancing correlative inhibition, but encourages development of lateral buds if the apical buds have declined in activity, whether naturally or as a consequence of treatment with such substances as maleïc hydrazide (Brian & Hemming, 1957).

Increase in internode length may be due mainly or entirely to increased cell extension, as in the garden pea (Brian & Hemming, 1955), but increase in the number of cell divisions may also be involved, as in *P. vulgaris* (Feucht, 1958; Greulach & Haesloop, 1958).

The magnitude of the response to gibberellin varies from species to species and from variety to variety within a species. The response is most marked in genetic dwarfs, as has been demonstrated in the garden pea (Brian & Hemming, 1955), maize (Phinney, 1956), rye-grass (*Lolium perenne* L.) (Cooper, 1958) and cotton (Ergle, 1957). As a result of treatment with gibberellin the dwarf assumes the appearance of the tall phenotype. Tall varieties of the same species respond only slightly or not at all.

(*b*) *Herbaceous plants sensitive to photoperiod*

The stem growth of most herbaceous plants is profoundly influenced by day-length. Such plants typically produce short internodes in short-day photoperiods and long-internodes in long-day photoperiods; the number of internodes may be greater in long-day conditions. The extreme case is found in those plants which grow in a rosette form in short-day photoperiods, with negligible formation of visible internodes, but develop long leafy stalks in long-day photoperiods. It should be noted that this general association of vigorous shoot growth with long-day photoperiods holds good irrespective of the flowering behaviour of the plants—plants in which flowering is induced by exposure to long-days and those which are induced to flower only in short-day photoperiods, all usually show maximum stem-development in long-day photoperiods.

Gibberellin treatment of plants kept in short-day conditions leads to vegetative developments similar to those induced by exposure to longer days. This has been shown for such long-day plants (in their flowering response) as species of *Adonis*, *Anethum*, *Crepis*, *Lactuca*, *Lapsana*, *Petunia*, *Polemonium*, *Raphanus*, *Rudbeckia*, *Samolus*, *Silene*, *Scabiosa* and *Spinacia* (Bünsow & Harder, 1956, 1957; Chaylakhian, 1957; Chouard, 1958*a*; Lang, 1957; Wittwer & Bukovac, 1957*a*). The short-day plant *Kalanchoë blossfeldiana* Poelln. also produces greatly enlarged vegetative shoots when treated with gibberellin, though flowering is inhibited, as also occurs if this plant is exposed to long-day conditions.

Thus, generally speaking, in such plants growing under short-day conditions, gibberellin induces vegetative developments characteristic of their development in long-day conditions. If it is applied to plants growing in long-day conditions the effects are usually smaller, suggesting that the effects of exogenous gibberellin and exposure to long-day photoperiods are essentially similar. Some exceptions to this generalization are mentioned in the next section.

The response to gibberellin may be considerably greater than the natural response to long-days. This depends to a great extent on the dose of gibberellin applied or on the frequency of application of doses. Sometimes quite novel developments are induced, a particularly interesting case being that of *Ramondia pyrenaica* Rich. This plant produces no leafy stem in nature, the flowers being borne on a leafless scape and all leaves borne in a basal rosette. If treated with gibberellin a leafy stem is produced (Chouard, 1958*a*).

(*c*) *Herbaceous plants which require vernalization for complete development*

Many long-day plants require exposure to low temperature for a critical period before maximum vegetative development takes place. Typical plants of this class are the biennials, which only pass from the rosette stage to formation of a leafy stalk when they are vernalized by low temperature treatment and subsequently exposed to long-day photoperiods. Lang (1956*a*, *b*, *c*) showed that gibberellin treatment would replace vernalization in *Hyoscyamus* and, since then, many other biennials have been shown to respond similarly, including species of *Apium*, *Brassica*, *Centaurium*, *Cichorium*, *Daucus*, *Digitalis*, *Euphorbia*, *Petroselinum* and *Scrophularia* (Bukovac & Wittwer, 1957; Carr, McComb & Osborne, 1957; Chouard, 1958*a*; Wittwer & Bukovac, 1957*b*).

Gibberellin will usually replace vernalization and allow development to proceed normally in plants kept in long-day photoperiods. It often has a much smaller effect in plants kept in short days, so that it appears that it will not always replace the effects of vernalization *and* long-day photoperiods; this has been shown in *Hyoscyamus* (Lang, 1956*a*, *b*) and *Centaurium minus* Moench. (Carr *et al.* 1957). This may only be a matter of finding the right magnitude and frequency of gibberellin dosage. Indeed, it is probably significant that large doses of gibberellin are needed to simulate vernalization. To induce marked shoot development in day-neutral dwarfs and in long-day plants doses of the order of a microgram of gibberellin per plant are usually sufficient, but to induce shoot formation in biennials doses nearer a milligram per plant are usually needed. Indeed, some vernalization-requiring species, notably *Reseda luteola* L., at first appeared not to respond at all to repeated doses of gibberellin (Chouard, 1958*a*) but eventually it was found that a stalk formed after a sufficiently large dose had been applied (Chouard, 1958*b*). Nevertheless, vernalization-dependent stem development of biennials and perennials can usually be induced by treatment with gibberellin.

(*d*) *Woody plants*

The pronounced seasonal character of growth in woody shrubs and trees is essentially a response to photo-period (Nitsch, 1957*a*; Wareing, 1956). Cessation of growth, dormancy of buds and leaf fall in deciduous plants are usually a response to the onset of shorter days in the autumn. This dormant condition is terminated in the spring by the return to longer days; in some cases exposure to low temperatures is also necessary. These stimuli, as in the examples of herbaceous plants discussed above, can in some cases be replaced by treatment with gibberellin; this has been demonstrated in *Acer*, *Camellia*, Elberta peach, *Paeonia* and some species of *Pinus* (Barton & Chandler, 1957; Bourdeau, 1958; Donoho & Walker, 1957; Lockhart & Bonner, 1957; Lona & Borghi, 1957; Nitsch, 1957*b*; Wareing, 1958). Three points of special interest have emerged from these investigations. (i) In some species, the similarity between the effects of gibberellin and exposure to long-day photoperiods is emphasized by the observation that growth is stimulated by exogenous gibberellin in plants kept in short days, but the already more rapid growth of plants transferred to long-day photoperiods is not further accelerated by exogenous gibberellin (Bourdeau, 1958). In other species the differential effect is less marked but the response to gibberellin is, nevertheless, greater in short-day photoperiods (Nitsch, 1957*b*). (ii) In *Acer pseudoplatanus* L. cambial activity of dormant shoots is only slightly stimulated by exogenous gibberellin and the new tissue formed consists of small unlignified cells. If indolylacetic acid is applied with gibberellin a wide zone of fully differentiated wood is formed, though indolylacetic acid alone has little effect (Wareing, 1958). (iii) No response to gibberellin of plants kept in short-day photoperiods has been detected with several woody species (Lockhart & Bonner, 1957; Nitsch, 1957*b*). It is possible that combinations of gibberellin and indolylacetic acid would have been effective, as in *Acer pseudoplatanus*.

(*e*) *Other examples of shoot dormancy*

The dormancy of potato-tubers is not related to photoperiod or any requirement for vernalization, but disappears gradually after the tubers are harvested. This type of dormancy too is broken by gibberellin treatment of the tubers. If growing plants are sprayed with gibberellin the buds on the tubers do not become dormant, so that highly deformed, branched tubers are produced (Brian, Hemming & Radley, 1955; Lippert, Rappaport & Timm, 1958; Rappaport, Lippert & Timm, 1957).

A dormant condition of shoots and fruits of Marglobe tomatoes, induced by too high a proportion of far-red in the incident light, can be relieved by spraying the plants with gibberellin solutions (Liverman & Johnson, 1957).

LEAF GROWTH

Effects of gibberellin on leaf-growth are available. Leaf size is unaffected in some plants, for example, in the garden pea. In others, for example, *Phaseolus* (Gray, 1957), Cupid sweet pea (Brian, Hemming & Lowe, 1959) and wheat (Brian, Elson, Hemming & Radley, 1954) leaf size may be considerably increased. In *Phaseolus* this is merely an acceleration of development, final leaf size being unaffected (Humphries, 1958) but in the Cupid sweet pea and wheat final leaf size is also increased.

Gibberellin induces expansion of discs cut from etiolated *Phaseolus* leaves and of sections of etiolated cereal leaves (Hayashi & Murakami, 1954; Radley, 1958). Natural gibberellins may therefore be of importance in control of mesophyll growth.

ROOT GROWTH

Gibberellin has little effect on root growth. High concentrations may slightly inhibit root extension (Brian *et al.* 1954, 1955; Sumiki, 1952; Yabuta & Hayashi, 1939*b*). Stimulation of root growth of intact plants has not been recorded, and of root sections only once (Whaley & Kephart, 1957). Root sections from dwarf peas which respond markedly to gibberellins in shoot growth show no response to gibberellin over a wide range of concentrations (Brian & Hemming, unpublished results). This apparent lack of effect of gibberellins on root growth is surprising, but further investigation may modify this picture.

Formation of adventitious roots on cuttings is strongly inhibited (Brian, Hemming & Radley, 1955). It has been suggested (Brian, 1957) that this might be a secondary effect caused by diversion of nutrients to the apex of the cutting, since gibberellin-treated stem cuttings may extend considerably. Further work has shown that this explanation is incorrect, and that there is a direct inhibition of the cell-divisions which would lead to the formation of the adventitious root initials.

Flowering

Gibberellin has little effect on the flowering of day-neutral plants, except to delay slightly or to accelerate the appearance of flowers. Its most clear cut effect is in induction of flowering of long-day plants kept in non-inductive short-day photoperiods or in replacing low-temperature exposure as a necessary pre-requisite to flowering of some biennials. In nature, flowering of such plants is associated with increased vegetative development, notably in production of a leafy stalk. Most of those species which respond to gibberellin vegetatively (see the section on stem growth above) also flower as a result of treatment. However, a minority of plants which respond vegetatively have not yet been induced to flower; these include Petkus rye (Lang, 1957), *Scrophularia vernalis*, *Iberis intermedia*, *Euphorbia lathyrus* L. (Chouard, 1958*a*) and winter wheat (Krekule & Martinovska, 1958).

Short-day plants have been less extensively investigated. Gibberellin treatment of *Kalanchoë blossfeldiana* kept in inductive short-day photoperiods leads to extensive vegetative development but flowering is inhibited. In fact the plant develops just as if it were exposed to long-day photoperiods (Harder & Bünsow, 1958).

Sexuality of flowers. Nelson & Rossman (1958) have shown that treatment of some lines of inbred maize with rather high concentrations of gibberellin applied as a plant spray, leads to a very high incidence of male sterility. Plack (1958) has shown that the effect of emasculation of *Glechoma hederacea* L. flowers (reduction of size of corolla as in natural female flowers) can be reversed by treatment with gibberellin.

Development of fruits and seeds

Pollen-tube growth. Gibberellin might indirectly affect fruiting by its effects on pollen-tube growth. In some species pollen-tube growth is accelerated and percentage germination in defined media increased by gibberellin (Chandler, 1957; Kato, 1955; Sumiki, 1955; Wada, 1949). In other species pollen-tubes are stunted and distorted by gibberellin (Chandler, 1957).

Flower dehiscence. Seed production by Cupid sweet peas is considerably enhanced by systemic treatment with gibberellin, a result mainly due to prevention of premature abscission of flowers (Brian *et al.* 1959).

Parthenocarpy. Parthenocarpic development of tomato fruit as a result of spraying the trusses with gibberellin solutions was first described by Wittwer, Bukovac, Sell & Weller (1957). Using a male-sterile Earlypak tomato, Persson & Rappaport (1958) have shown that the effect is systemic, parthenocarpic fruit-set being increased even where gibberellin is applied to the roots by soil-treatment, or applied to expanded leaves or the stem apex.

Fruit swelling. Liverman & Johnson (1957) showed that swelling of 'dormant' tomato fruits was enhanced by gibberellin treatment. More recently, remarkable enlargement of berries of two varieties of seedless grape has been shown to follow gibberellin treatment (Weaver, 1958). Fruit swelling has for some time been known to be associated with auxin production by the immature seeds in the fruit. Weaver has pointed out that it now seems possible that gibberellins may also be involved, since immature seeds are known to be particularly rich sources of these hormones (Phinney *et al.* 1957; Radley, 1958). Indeed, in an investigation of growth-promoting substances in bean (*Phaseolus vulgaris*) seeds at various stages in the development of the seed, Nitsch & Nitsch (1955) detected two growth-promoters present at maximum concentration in the immature seed, declining in concentration as the seed matured. One of these was identified as indolylacetic acid; the other substance, judging by its behaviour on chromatograms, could well be gibberellin A_1, which has since been identified as a constituent of *Phaseolus* seeds (see Introduction).

SEED GERMINATION

Gibberellin overcomes seed-dormancy in many cases. This includes the dormancy of light-requiring seeds, such as lettuce (Kahn, Goss & Smith, 1957; Lona, 1956) and *Kalanchoë* (Bünsow & von Bredow, 1958) and of seeds normally requiring low-temperature treatment, e.g. certain species of *Malus* (Barton, 1956). These effects are in line with light-simulating and vernalization-simulating effects described in earlier sections of this paper. But seed dormancy is undoubtedly biochemically complex. Thus, Skinner & Shive (1958) have demonstrated synergistic effects between gibberellin and kinetin in stimulation of lettuce seed germination, and Pollock (1958) found that dormant barley grain responded to gibberellin, kinetin and hydrogen sulphide, with a particularly striking synergism between hydrogen sulphide and gibberellin with some samples of grain.

DEVELOPMENT OF LOWER PLANTS

Though little work has yet been reported, it is clear that gibberellin may have profound effects on the development of lower green plants, though fungi are unaffected. Among effects observed are promotion of elongation of the filaments of germlings of the Alga *Ulva lactuca* (Provasoli, 1957) and of moss protonemata (von Maltzahn & MacQuarrie, 1958); in the latter case increases of both cell multiplication and cell elongation are involved. A particularly interesting observation concerns the elongation of the dormant sporogonial setae of the liverwort *Pellia epiphylla* L. The sporogonium is fully differentiated early in the winter but elongation of the setae does not take place until February or March onwards; this is apparently a photoperiodic response. The dormant setae extend immediately if the plants are sprayed with gibberellin (Asprey, Benson-Evans & Lyon, 1958). Wardlaw & Mitra (1958) have demonstrated formative effects of gibberellin on shoot apices of the fern *Dryopteris austriaca* (Jacq.) Waynar.

DISCUSSION

(*a*) *Interrelations of gibberellins and indole-auxins*

It will be clear from the foregoing account of the physiological responses to exogenous gibberellin that the gibberellins have properties in many ways distinct from those of indolylacetic acid and other indole-auxins, and there is much further evidence for this view (Brian, 1958; Brian & Hemming, 1958; Brian *et al.*, 1955; Kato, 1953, 1958). Brian & Hemming (1958) have presented evidence that, in its effects on extension of pea internodes, gibberellin is dependent on the presence of indolylacetic acid. A similar dependence on the presence of indolylacetic acid has been demonstrated by Kuse (1958), using a technique based on extension of petioles of *Ipomoea batatas* Poir., by Asprey *et al.* (1958) using isolated sporogonia of *Pellia epiphylla* and by Wareing (1958) in his work on cambial activity in *Acer pseudoplatanus*. Thus where gibberellin has an effect on vegetative growth when applied alone we may assume that sufficient endogenous indole-auxin is already present; this view is supported by the work of Purves & Hillman (1958) using pea sections at various distances from the apex, thus containing varying concentrations of endogenous auxin, and by similar work of Radley (1958) with sections of the first true leaf of wheat seedlings.

It is not improbable therefore, that in other effects on plant development, gibberellin acts in association with the indole auxins. This view is supported by what little we know of its distribution in plant tissues. Naturally occurring gibberellin-like materials are particularly abundant in young developing seeds, as also are the indole-auxins, and their concentration declines as the seeds mature, just as indole-auxins also decline in concentration. Radley (unpublished results) has found gibberellin-like substances particularly abundant in young leaves of *Phaseolus*, declining in concentration as the leaves expand, which is very similar to the distribution of indole-auxins in seedling leaves.

(*b*) *Role of gibberellins in responses to photoperiod*

The responses of plants to exogenous gibberellin, reviewed in earlier sections of this paper, enable us to make some assessment of the probable role of the gibberellin-like hormones now known to be present in plants. Here I propose particularly to discuss responses of plants to photoperiod and vernalization, dealing first with vegetative responses, and then with flowering responses.

The data presented above reveal a remarkable parallelism between the effects of exogenous gibberellin and the effects of exposure to long-day photoperiods. This is particularly true of vegetative responses, of both herbaceous and woody higher plants, and of the extension of sporogonial setae of the liverwort *Pellia epiphylla*. There is also a striking similarity between the vegetative effects of exogenous gibberellin and those of exposure to low temperature in such plants as biennials. A hypothesis that would satisfactorily explain most, if not all, vegetative responses to photoperiod would be that gibberellins are formed in plant tissues in light and reversibly decay to an inactive precursor in darkness so that the longer the photoperiod the greater the concentration reached (Brian, 1958, 1959). Similarly, the vegetative responses to vernalization could be interpreted as the result of activation of gibberellin-synthesizing systems. These hypotheses are strongly but indirectly supported by what we know of the effects of exogenous applications of gibberellin, but no direct evidence, from measurements of endogenous gibberellin levels, is yet available.

There are some experimental observations which may appear to be at variance with the hypothesis, and which therefore need further consideration. Some biennials have failed to respond to gibberellin as they do to vernalization; the dormant shoots of some woody plants in short-day photoperiods have also failed to respond to gibberellin. It seems to me highly probable that such cases will be found to respond if the gibberellin dosage is adjusted, as was found to be the case with *Reseda luteola* (Chouard, 1958*a*, *b*), or if gibberellin is used in combination with an indole auxin, as was found to be effective in inducing cambial activity in dormant *Acer* twigs (Wareing, 1958). Thus vegetative responses to photoperiod and to vernalization can be plausibly explained in terms of gibberellin synthesis, bearing in mind that here, as in simpler growth responses to gibberellin, an interaction with the effects of indole auxins is also probably involved.

Flowering responses cannot be satisfactorily explained on so simple a basis, though the frequent association between vegetative growth and flowering in long-day plants, whether induced by long-day photoperiods or by exogenous gibberellin, points to a related mechanism.

Considering first of all long-day plants, we find that most of them, if treated with gibberellin, will form a flower stalk and flowers even if kept in short day photoperiods. Similarly, exogenous gibberellin treatment in most cases will induce flowering of biennials, without vernalization, though less regularly than such a treatment induces formation of a stalk. Thus in general outline the flowering response of long-day plants to exogenous gibberellin is parallel to the vegetative response. However, there are some divergent observations that require explanation:

(i) Some biennial long-day plants will flower if treated with gibberellin and kept in long-day photoperiods, but not if kept in short-day photoperiods, e.g. *Hyoscyamus niger* L. (Lang, 1956*b*). This is not always the case, and it seems to me likely as I have already suggested, that a suitable gibberellin dosage regime will be found to induce flowering in such cases.

(ii) Whereas vernalization of biennial long-day plants kept in long-day photoperiods leads to a more or less simultaneous differentiation of a stalk and flower primordia, gibberellin treatment sometimes (but not in all species) leads to a separation in time between these two effects, so that a considerable development of stalk takes place before flower primordia are formed, e.g. in *Hyoscyamus* (Lang, 1957; Sarkar, 1958), and Sarkar (1958) has in consequence concluded that the hypothetical hormone 'vernalin' postulated by Melchers (1939) to be formed as a result of vernalization, cannot be identical with gibberellin. I do not think this conclusion is really warranted; it seems to me unlikely that application of exogenous gibberellin need necessarily *exactly* simulate the effects of endogenously produced glibberellin-like hormone, since the precise responses must depend on concentration levels and concentration gradients within the plant, difficult to achieve by exogenous application. Lang (1957) has suggested that the partial separation of the vegetative response of *Hyoscyamus* to gibberellin from its flowering response, indicates that the effect on flowering may be indirect. Indeed, there is experimental evidence that vegetative and flowering responses of long-day plants to photoperiod or to vernalization are separable. For example, Parker, Hendricks & Borthwick (1950) showed that increasing the number of long-day photocycles in induction of flowering of *Hyoscyamus* to levels in excess of that required to induce a complete flowering response, resulted in increased stem extension. Murneek (1940) showed that if *Rudbeckia bicolor* Nutt. is grown in long-day photoperiods throughout its life, it produces flowers on long-stems; if after the necessary critical period for induction of flowering it is returned to short-day conditions, flowering proceeds normally but stem extension is much reduced. In other words, the flowering response has a relatively short critical induction period, characteristic of the species, but vegetative growth is quantitatively related to the number of long-day photoperiods to which the plant is exposed with no clear-cut critical period.

Thus it seems to me that the flowering response of long-day plants to photoperiod can be brought into line with the explanation offered above for the vegetative response by supposing that gibberellin is produced in the plant as a response to light, vegetative growth being proportional to the amount of gibberellin formed and hence to the total length of the light exposure, but that the flowering response is induced as a result of maintenance of certain critical levels of the gibberellin in the plant for a critical period. This explains the possibility of experimental separation of the two effects. Responses to vernalization can be similarly explained.

This view enables us to explain the responses of short-day plants with little further elaboration. Long-day photoperiods stimulate vegetative development of short-day plants but inhibit flowering. The little experimental evidence at present available indicates that gibberellin has a similar effect. Here we must assume that the induction of flowering only takes place if levels of gibberellin are maintained for a critical period below a certain critical level, a level which would be exceeded if the plant were exposed to long-days.

Thus, to summarize, I am suggesting that vegetative responses to photoperiod are governed directly by the influence of gibberellins, or similar substances, formed in the plant as a result of exposure to light, whereas flowering is governed by a further reaction which is itself influenced by the endogenous gibberellin level. More concretely, supposing that a flowering hormone, 'florigen', common to short-day and long-day plants, does really exist, then in long-day plants its formation is dependent on maintenance of relatively high endogenous gibberellin levels for a critical period, and in short-day plants it is dependent on the maintenance of relatively low endogenous gibberellin levels for a critical period.

This is all frankly speculative, but is in good agreement with all we know of the effects of exogenous gibberellin on vegetative development and flowering. It is at least a reasonably useful hypothesis on which to base further experimental work.

(c) *Genetic dwarfs*

The relationship between genetic dwarfs and their tall counterparts is in some ways analogous to the relationship between photoperiodically sensitive plants growing in short- and long-day photoperiods respectively. I have tentatively explained the latter relationship in terms of gibberellin metabolism, biosynthesis being more active in long-day conditions. Similarly, genetic dwarfs, particularly since they assume the appearance of a tall phenotype if treated with gibberellin, could be interpreted as having a genetic failure in gibberellin metabolism. Indeed, some such reasoning as this was behind the successful search for gibberellin-like hormones in higer plants. However, Radley (1958) has failed to find any great difference in content of gibberellin-like hormones between dwarf and tall peas. This may be due to imperfections in extraction technique, but the result does emphasize the need for direct evidence for the explanation of responses to photoperiod proposed above.

However, while caution is necessary, the general impression obtained from the mass of experimental information on physiological effects of gibberellin now accumulating, is that we may be very near to a much closer understanding of the biochemical control of development of higher plants than we were before the discovery that the gibberellins are natural plant constituents.

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Some growth responses to gibberellic acid. By M. Y. Stant.

Jodrell Laboratory, Royal Botanic Gardens, Kew

During the summer of 1958, a number of plants were grown to study their reaction to gibberellic acid. We are indebted to Plant Protection Ltd., Fernhurst, who provided the pure substance. Plants were divided numerically into two sets. In one set the controls were sprayed with distilled water. The other set was sprayed weekly, from May to September, with a 100 p.p.m. aqueous solution of gibberellic acid (GA), containing a wetting agent. The solution was applied as a fine spray with an atomizer until the leaf surfaces became thoroughly wet.

The following species are amongst those that were treated: *Gossypium hirsutum* L., *Hibiscus cannabinus* L., *Corchorus olitorius* L., *Cannabis sativa* L., *Zebrina pendula* Schnizl. and *Plantago media* L. As soon as the plants showed any visible response to the treatment, they were subjected to a series of measurements designed to show that quantitative differences in size and form of plant organs had been produced by the gibberellic acid.

The following dimensions were taken: (1) total height measured from soil level to shoot tip; (2) stem diameter; (3) internode length (internodes were measured from the base upwards as the interval between successive nodes, the first internode being taken from the soil level to the first node); (4) number of internodes; (5) length of leaf or lamina; (6) breadth of leaf or lamina, l/b is the length/breadth ratio of the leaf or lamina, which gives a measure of shape; (7) petiole length; (8) length of axillary, or lateral shoot.

Results

Height. All plants showed an increase in shoot height. Treated plants of *Cannabis sativa* were 250 % taller than controls after 5 months. A difference generally becomes apparent within a week of spraying and is a measurable quantity after 2 weeks. The growth difference could be brought about in two possible ways: (1) by extending the length of individual internodes; (2) the internode length may remain unaltered and the stem become extended by the production of extra internodes at the apex. In all plants studied, both these factors combine to produce the total increase in shoot length.

Internode number. After several months the number of internodes doubled in *Gossypium hirsutum*, which has a high internode number. An increase of 10–25 % is more usual, and *Cannabis sativa*, for example, shows little difference in this respect.

Internode length. The average internode length for the whole plant increased as much as 300 % in *Cannabis sativa*, and up to 20 % in *Gossypium hirsutum*. A general increase of 60–100 % is more frequent. The mean percentage increase in internode length added to that of internode number gives a value approximating to the mean percentage increase in shoot height for each species.

A study was also made of internode length in relation to position in the shoot, or order of initiation. Internodes were numbered from base to apex, the order of inception, and the mean length of each internode for all the plants of the control set compared with its equivalent in the treated set.

Stem diameter. The taller treated plants usually have narrower stems. GA produces a decrease in stem diameter which is greatest in the initial stages of elongation. If development proceeds further, and spraying continues to produce a large replica of the control plant, a final increase in stem diameter may occur.

Leaf size. GA stimulates production of leaf material, as measured by size. The mean area/leaf increased by a regular 11 % in *Zebrina pendula*, and by 40 % in *Corchorus olitorius*. *Gossypium* and *Hibiscus* showed a decrease in mean area/leaf but an increase in average leaf area/plant.

Dimensions of the leaf were also affected by spraying. *Length* showed an increase of the order of 10 % for most species. *Breadth* varied in its reaction. It always showed a considerable decrease in *Hibiscus*, but the difference was smaller and less constant in other species, and readings of breadth increase were obtained occasionally.

Leaf shape, as measured by the length/breadth ratio, showed a constant change. This proportion increased with time. Older plants had longer and narrower leaves than the same species earlier in development. But at all stages of development spraying with GA raises this proportion by an amount which can vary from 10 to 100 %. This represents a considerable change in leaf shape.

Form. There is a general change in leaf form associated with GA in all plants studied at Kew. But the final form of the plant as a whole does not show any spectacular changes. Treated plants became larger and more elongated in shape. Sprayed plants of *Zebrina pendula* became rather straggly in appearance, but they were all very recognizably the same plants as the controls. The difference is one of size and proportion rather than form.

Plantago media, the only rosette plant to be treated, was exceptional because not only was the size of its leaves increased when sprayed with GA, but the plant became more erect in habit, and its rosette form was lost.

Petiole length does not seem to conform to the general theory that GA stimulates longitudinal growth. Results so far suggest that this dimension is often reduced in treated plants.

Axillary shoot length. GA retards lateral growth at first. Although axillary buds develop earlier in control plants, measurement of the length of lateral shoots of mature plants showed that GA increases the length and number of lateral shoots.

Flower and fruit. There is slight evidence that GA increases the number of flowers and fruits developed by each plant.

The picture then emerges of GA as a general growth stimulator, increasing the dimensions of the various morphological units of the plant. It should, however, be added here that control plants usually appeared in better condition. Treated plants produced softer, sometimes chlorotic, leaves, and their stems were less rigid. This could very probably be offset by additional feeding and spraying the leaves with sucrose solution, if GA is to be used to accelerate growth.

Discussion

Dr Stant's paper was discussed by Professor J. P. Hudson who said: Gibberellic acid appears to have increased the growth of species such as cotton and hemp under the sub-optimal conditions of a British glasshouse, in which it is difficult to grow such species well. It may prove that gibberellic acid, and other growth regulators, can be used in many ways to induce crop plants to produce heavier yields under sub-optimal climatic conditions. Indeed, the use of chemical stimuli to 'break the grip of the weather' on field crops may well develop into one of the most important advances in agronomy in our generation, opening up an entirely new field of endeavour in agricultural practices.

The effect of very long days on the flowering of winter rye. By O. R. Jewiss, F. G. Gregory and O. N. Purvis. Research Institute of Plant Physiology, Imperial College of Science and Technology, London

(With 2 Text-figures)

Previous work had shown that unvernalized Petkus winter rye fails to produce ears in normal summer days of 17 hr. light, whereas when grown in continuous light shooting and earing occur. After vernalization for a period of 6 weeks, normal ear production occurs in a photoperiod of 17 hr., and is only accelerated to a small degree in continuous light. The paper read at the symposium dealt with a full analysis of the flowering behaviour of unvernalized and vernalized winter rye grown in photoperiods varying from 17 to 24 hr. The photocycles employed comprised varying periods of daylight, of artificial light and of darkness in each 24 hr. Four series of experiments were carried out, of which the details of the photoperiodic regimes are shown in the above diagram (Fig. 1). Darkness is represented by fully black segments, artificial light by stippling and full daylight by white segments. The light stippling indicates a light intensity of 300–500 f.c. and the heavier stippling 30–40 f.c. respectively.

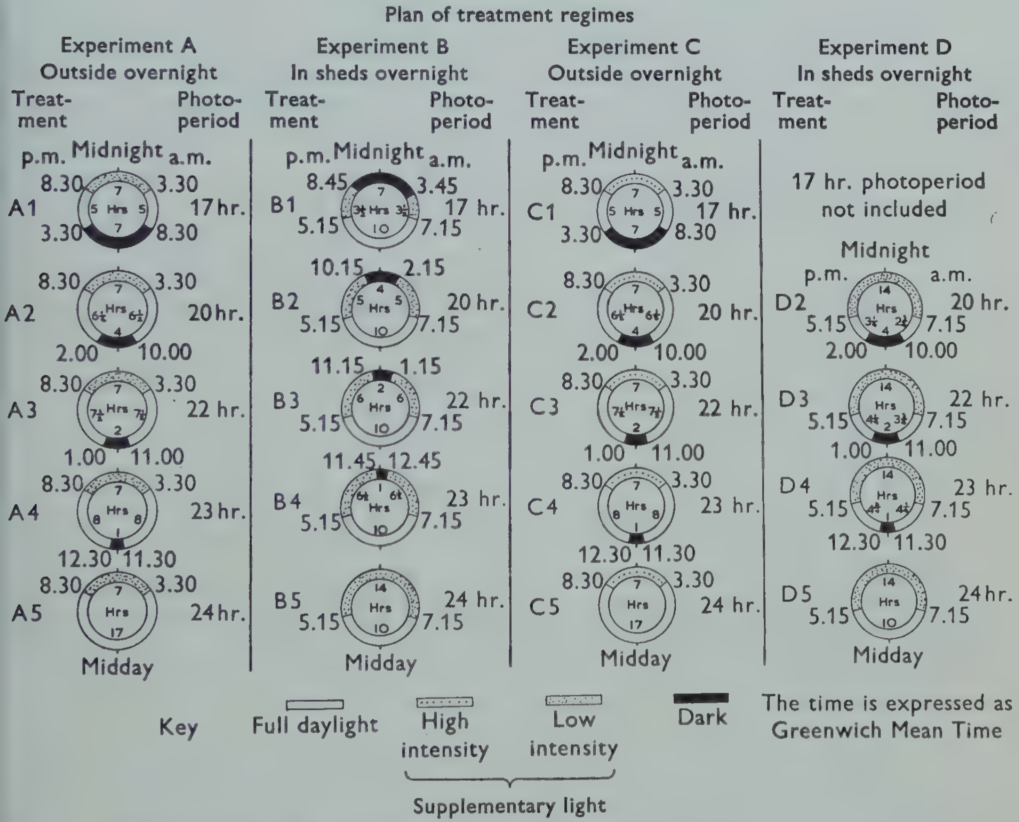

Plan of treatment regimes
Experiment A
Outside overnight
Experiment B
In sheds overnight
Experiment C
Outside overnight
Experiment D
In sheds overnight
Treatment
Photoperiod
p.m. Midnight a.m.
A1 8.30 3.30 3.30 8.30 17 hr.
A2 8.30 3.30 2.00 10.00 20 hr.
A3 8.30 3.30 1.00 11.00 22 hr.
A4 8.30 3.30 12.30 11.30 23 hr.
A5 8.30 3.30 24 hr.
B1 8.45 3.45 5.15 7.15 17 hr.
B2 10.15 2.15 5.15 7.15 20 hr.
B3 11.15 1.15 5.15 7.15 22 hr.
B4 11.45 12.45 5.15 7.15 23 hr.
B5 5.15 7.15 24 hr.
C1 8.30 3.30 3.30 8.30 17 hr.
C2 8.30 3.30 2.00 10.00 20 hr.
C3 8.30 3.30 1.00 11.00 22 hr.
C4 8.30 3.30 12.30 11.30 23 hr.
C5 8.30 3.30 24 hr.
17 hr. photoperiod not included
D2 5.15 7.15 2.00 10.00 20 hr.
D3 5.15 7.15 1.00 11.00 22 hr.
D4 5.15 7.15 12.30 11.30 23 hr.
D5 5.15 7.15 24 hr.
Hrs
Midday
Key
Full daylight
High intensity
Low intensity
Dark
Supplementary light
The time is expressed as Greenwich Mean Time

Fig. 1. Diagram showing light regimes during each 24 hr. cycle. Fully black segments = hours of darkness. Heavy stippling = hours of artificial light 30–40 f.c. Light stippling = hours of artificial light 300–500 f.c. White segments = hours of full daylight.

The effect of the treatments on final leaf number and on 'score' (progress to flowering) in the vernalized and unvernalized series is shown in Fig. 2. A score of 21 indicates that the plant has reached the stage of flower initiation (appearance of double ridges), higher scores show the degree of development of spikelets beyond this stage. The figures along the curves indicate the number of hours of full daylight received in each cycle.

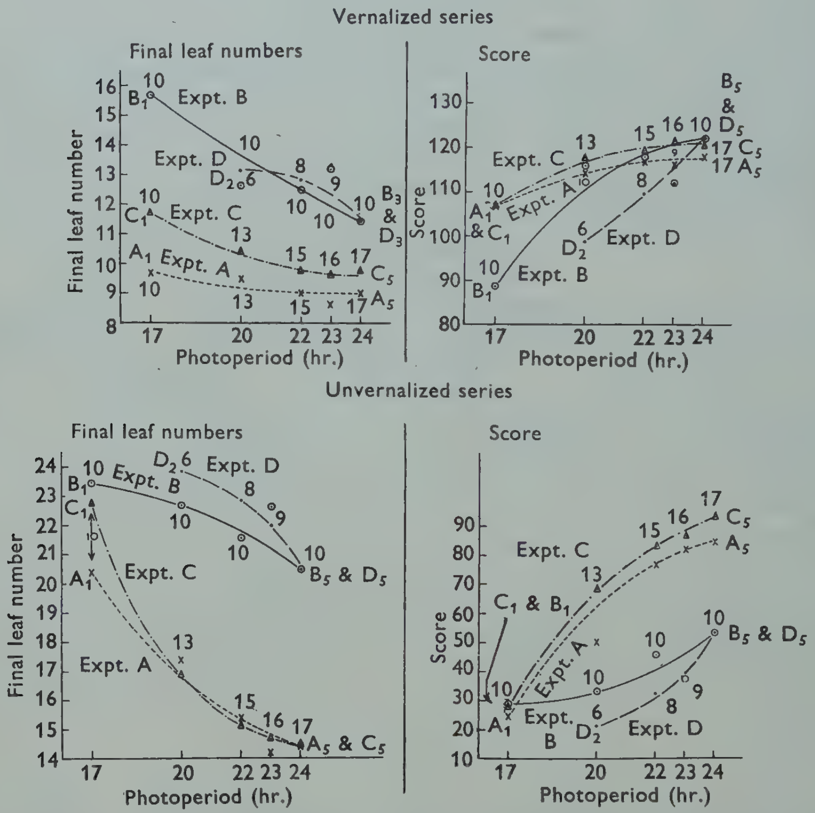


Fig. 2. The effect of very long days (natural daylight supplemented by artificial light) on the final leaf numbers and on the 'scores' of vernalized and unvernalized Petkus winter rye. Details of the treatments 'A', 'B', 'C', and 'D' are given in Fig. 1. Key: ×----× Expt. A; ⊙——⊙ Expt. B; △—·—△ Expt. C; ·——· Expt. D. The figures on the curves represent the total number of hours full daylight received in each photoperiod. All curves are drawn freehand.

In both the unvernalized and vernalized series the effect of duration of the photoperiod on score is evident, as also is the predominant effect of increasing hours of bright light at any one photoperiod. In 17 hr. photoperiods there is no effect of treatment on score of the unvernalized series in which all plants have reached the stage just beyond flower initiation, so that in all other photoperiods the effect of the treatment is concerned with post-initiation stages. As the photoperiod is increased in the unvernalized series, the curves diverge, and a maximum difference in score is found in continuous light. By contrast, in the vernalized series, in which the score ranges from 90 upwards, the maximum differences in score are seen in the 17 hr. photoperiods, and all the curves converge as the photoperiod increases. In the absence of darkness (sets A5, B5, C5 and D5 10 hr. of full daylight are as effective as 17 hr., indicating that the duration of full daylight is not a limiting factor in the vernalized series, while evidently the hours of bright light are the determining factor in the unvernalized series. The data for final leaf number presents an inverse relationship to scores.

At the symposium these data were interpreted in terms of a schema already published (Gott, Gregory & Purvis, 1955).

REFERENCE

Gott, M. B., Gregory, F. G. & Purvis, O. N., 1955. Studies in vernalisation of cereals. XIII. Photoperiodic control of stages in flowering between initiation and ear formation in vernalised and unvernalised Petkus winter rye. *Ann. Bot., Lond.*, N.S., **21**, 87–126.

Some effects of environment and hormone treatment on reproductive morphogenesis in the Chrysanthemum. By W. W. Schwabe. Research Institute of Plant Physiology, Imperial College, London

(With Plate **10** and 2 Text-figures)

INTRODUCTION

The study of morphogenesis in the plant is mainly concerned with the events at the growing points. In the higher plants, in the vegetative condition, the active stem apices give rise to the leaves and their associated lateral buds, and their initiation and development follow a regular sequence which, under normal circumstances, is not easily disrupted—except by surgical and other drastic techniques. The positioning of the young primordia, their size at initiation relative to the main growing point and their rate of growth, determine the phyllotactic pattern and also to some extent the general appearance of the plant. When the plant becomes reproductive there is a change to an entirely different sequence which is equally regular and fixed. In contrast to the leaf, the flower primordium represents an axial structure and in many instances it may be regarded as a precocious lateral bud.

While the onset of reproduction frequently leads to the formation of modified leaves or bracts before the actual flower primordia arise, this is only a very transitory phase and each growing point must follow either one or other main sequence, and it is not possible for it to persist in producing intermediate structures. This in itself indicates that when reproduction starts, there is a complete switch-over at the apex from one morphogenetic pathway to another. It is this fact which has also served to justify the concentration of research on the actual 'initiation' of flowering; clearly it is 'le premier pas qui coûte'.

Once reproductive development has begun, the growing point affected must either continue this new line of development or finish; only in relatively rare teratological instances is a return to the earlier sequence possible. Experimentally, it is, of course, possible to modify the various stages of floral or reproductive development also, but under normal conditions this does not usually take place.

Confining attention to the Chrysanthemum, first consideration is to be given to what is known about the behaviour of the vegetative apex, which factors of the environment, etc., are known to affect the transition from the vegetative line of development to the reproductive, and what changes have been observed to occur at the apex during this stage. Finally, the factors influencing the later stages of reproductive development will be discussed. It must be stressed, however, that in a plant of such horticultural interest as the Chrysanthemum large numbers of different varieties have been selected—often specifically for differences in their physiological behaviour. Hence, varietal differences in response must be pronounced and not all the factors to be discussed will be of equal importance in all strains. In most of the experimental work to be described, the variety 'Sunbeam' was used, and it is believed that this variety is relatively unselected and perhaps nearer to the 'wild type' of Chrysanthemum than many other varieties.

A. THE VEGETATIVE GROWING POINT

The vegetative growing point of the Chrysanthemum is seen in Pl. **10**, after all young leaf primordia have been cut away. The bare apex, unoccupied by such primordia, is approximately 150 μ in diameter, and its mean area remains relatively constant throughout the period of vegetative growth. During this period it cuts off leaf initials at a regular rate. At initiation the area of each primordium is approximately equal to the transverse area of the bare apex itself as determined by Evington (1954), using the methods evolved by Richards (1948, 1951).

The rate of primordium formation during vegetative growth may vary from 2·2 to 3·2 per week, i.e. defining the rate of initiation at the apex as the 'true plastochron' this varies from 3·2 to 2·2 days. The variation is due to the fact that the previous history of the plant and also the prevailing environment can affect this rate. The effects of a variety of factors and their combinations have been investigated; one of the most important being the temperature history of the plant, i.e. whether it has been vernalized or not. Determinations of the 'true plastochron' for plants grown in identical conditions, but of different temperature history yielded the following values:

Unchilled control	3·18 ± 0·18 days
2 weeks chilling	2·44 ± 0·13 days
4 weeks chilling	2·26 ± 0·18 days

The actual growth temperature does not appear to affect the 'true plastochron' very much, regardless of whether the temperature is held constant or whether different day and night temperatures are given, as will be seen below from the data of two experiments:

Constant day and night temperature	Day temperature	Night temperature
17° C., 2·79 days	17° C., 2·25 days	17° C., 2·29 days
22° C., 2·54 days	22° C., 2·14 days	22° C., 2·25 days
27° C., 2·69 days	27° C., 2·25 days	27° C., 2·10 days

This relative independence of temperature applies, however, only to the 'true plastochron', i.e. the actual rate of leaf primordium initiation as determined by dissection of the buds.

The 'apparent plastochron', i.e. the rate of unfolding of new leaves from the bud, as determined by leaf counts, is affected very much more by the actual growth temperature, and the following values were determined in one experiment:

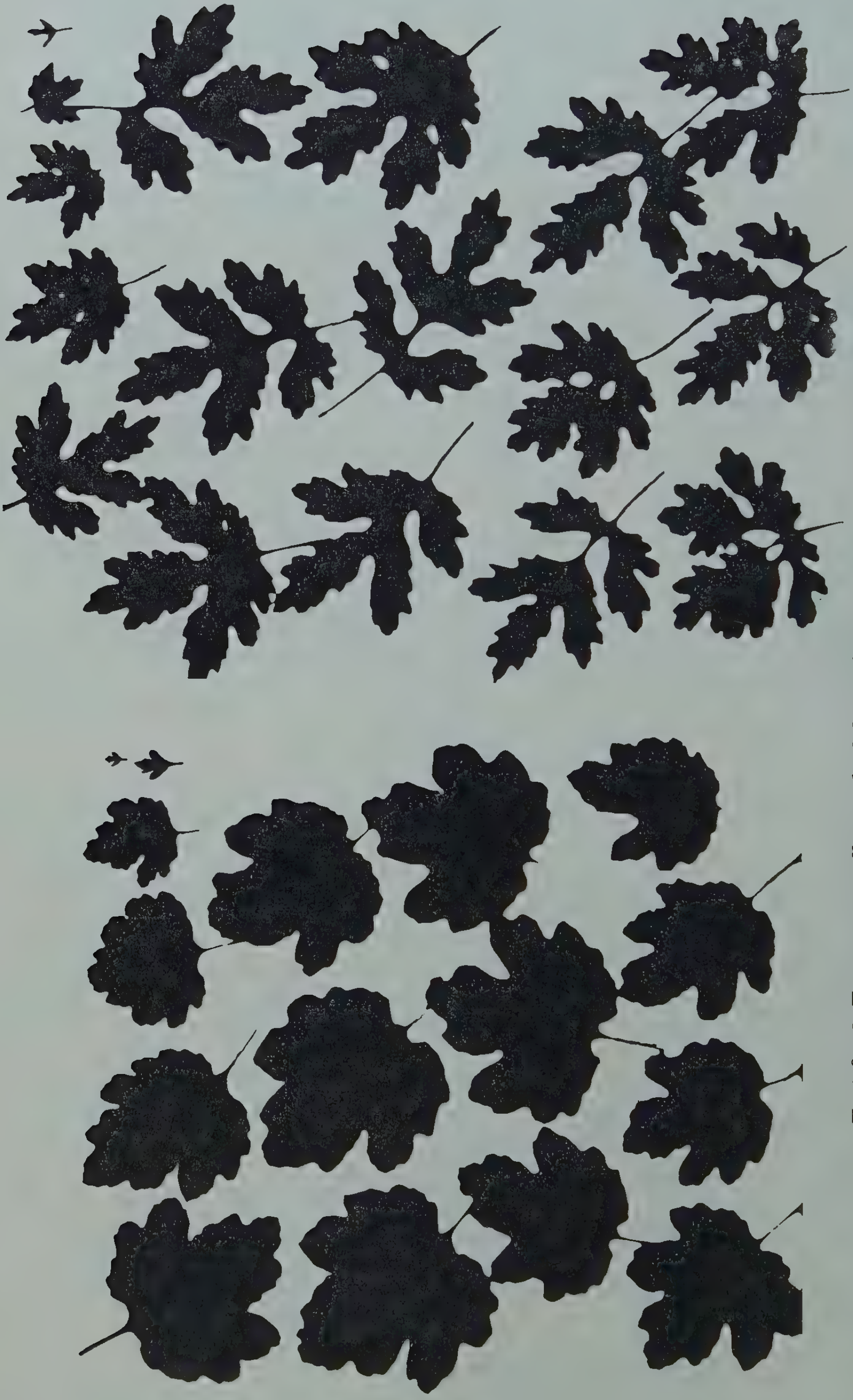
$$\left.\begin{array}{l}18^\circ\text{ C., }3{\cdot}86\text{ days}\\ 22^\circ\text{ C., }3{\cdot}02\text{ days}\\ 26^\circ\text{ C., }2{\cdot}61\text{ days}\end{array}\right\}\ \pm 0{\cdot}18$$

The marked difference between these two measures is due to the fact that at lower temperatures more leaves are accumulated in the terminal bud which then do not expand as rapidly as they are initiated. Internally there is, of course, some heat production in the bud, and the apex within it is also relatively well insulated by layers of air between the primordia. Therefore, a mechanism retarding expansion of the outer primordia might perhaps serve as a homoeostatic regulator allowing the growing point itself to be at a somewhat different temperature from the outer environment. However, this suggestion is purely speculative, and in fact it seems doubtful whether it could quantitatively account for the observed effect.

Before leaving the discussion of the behaviour of the vegetative apex, brief reference may be made to the fact that the morphology of the young primordia themselves is also determined at an early stage in the bud. The external environment is also capable of modifying their final shape while acting at an early stage in their ontogeny. A good example of this is seen in the temperature effect on leaf shape. In the Chrysanthemum the degree of dissection varies very much with the temperature prevailing during initiation. Leaves initiated at relatively high temperature (27° C.) become very much less dissected than those formed at a lower temperature (17° C.). (Text-fig. 1.)

B. THE CHANGE-OVER TO THE REPRODUCTIVE CONDITION

(i) *Effects of the environment.* In the Chrysanthemum, as in so many other plants, the onset of reproductive development is largely subject to control by the environment. The actual conditions required have been fairly closely studied and at least for the



Text-fig. 1. Temperature effect on leaf shape. Leaves arranged in order of their ages. Left: from a plant grown at 27° C.; right: from a plant grown at 17° C.

variety 'Sunbeam' are now known in considerable detail. It must be stressed, however, that other Chrysanthemum varieties are likely to show at least quantitative differences from the optimum values established.

For brevity's sake, the various factors controlling the switch-over to the reproduction condition and its continuation have been summarized in tabular form (Table 1), which also shows the effective ranges of duration and level.

Table 1. *Sequence of factors controlling the initiation of reproductive development in the Chrysanthemum, and their optimum levels and duration*

(Variety 'Sunbeam')

Factor	Level	Duration	Reference
Low temperature (vernalization)	1°–12° C.	3–4 weeks	Schwabe, 1950
Growth temperature Day Night	22°–23° C.	Until flowering	Schwabe, Unpubl.
Long-day treatment	16 hr. day	3–4 weeks	Schwabe, 1952*a*
Short-day treatment	8–10 hr. day	From then on till flowering	
Light intensity during growth period	> Approx. 1500–2000 f.c.	Throughout	Schwabe, 1952*b*

This table represents, of course, an oversimplification, since there are numerous interactions between the various factors. As regards their seat of action, it is also known that those conditions involving the light factor, i.e. light intensity and duration, etc., are perceived by the leaves. On the other hand, grafting experiments and experiments in which different parts of the plants were subjected to different temperature conditions have shown that the vernalization effect is perceived in the growing point itself. The physiological changes wrought there persist only in the meristem and are not translocated about the plant through mature tissue, but they may increase in parallel with apical growth and in this way be passed on to newly arising axillary meristems (Schwabe, 1954).

(ii) *Internal and nutritional factors.* Not much is known as yet about the internal factors involved in the onset of flowering. Nitrogen content, as controlled by the level of this nutrient in the culture medium, has only a slight effect by accelerating or, when deficient, retarding growth generally. In one experiment nitrogen-deficient plants budded a mere 4 days earlier than the controls with full nutrient supply, and the number of leaves produced prior to bud formation was actually lower than in the controls. Also chromatographic analysis of the growing points of vegetative and budded plants did not reveal any marked differences in the free amino acids present.

Carbohydrate level also seems to be of little importance for the vernalization processes accelerating flowering in this plant. This was revealed in some experiments on the de-vernalization of the Chrysanthemum. Such de-vernalization can be achieved by prolonged exposure to low light intensity treatment (Schwabe, 1957*b*), a treatment which serves, of course, to deplete the carbohydrate reserves of the plant very severely indeed. In plants so treated stem growth and leaf expansion are brought almost to a complete halt. Nevertheless, such starved plants can be completely re-vernalized at once by a second chilling period while still in the starved condition. Also, while application of soluble carbohydrate to such plants will permit stem growth and leaf expansion to continue, it will not avert the de-vernalizing effect. Hence the role of carbohydrate in the vernalization process is at best subordinate.

(iii) *Hormones.* As regards hormones there is now some evidence that their application may delay or hasten the transition to the flowering condition. The initiation of reproductive development may be delayed by indole-3-acetic acid in lanolin paste if this is applied repeatedly just below the terminal growing point, even when the plant is fully vernalized. In one experiment six such applications of paste delayed bud formation by three weeks and caused the auxin-treated plants to produce on the average an additional six leaves before budding.

Gibberellic acid,[1] on the other hand, applied in solution to the young leaves was shown to induce a proportion of plants to flower even in the absence of any chilling treatment, as will be seen from Table 2, but the effect was very slight, when leaf number figures are considered, compared with that of vernalization. Other synthetic growth substances such as triiodobenzoic acid do not appear to affect the onset of the reproductive phase to any significant extent.

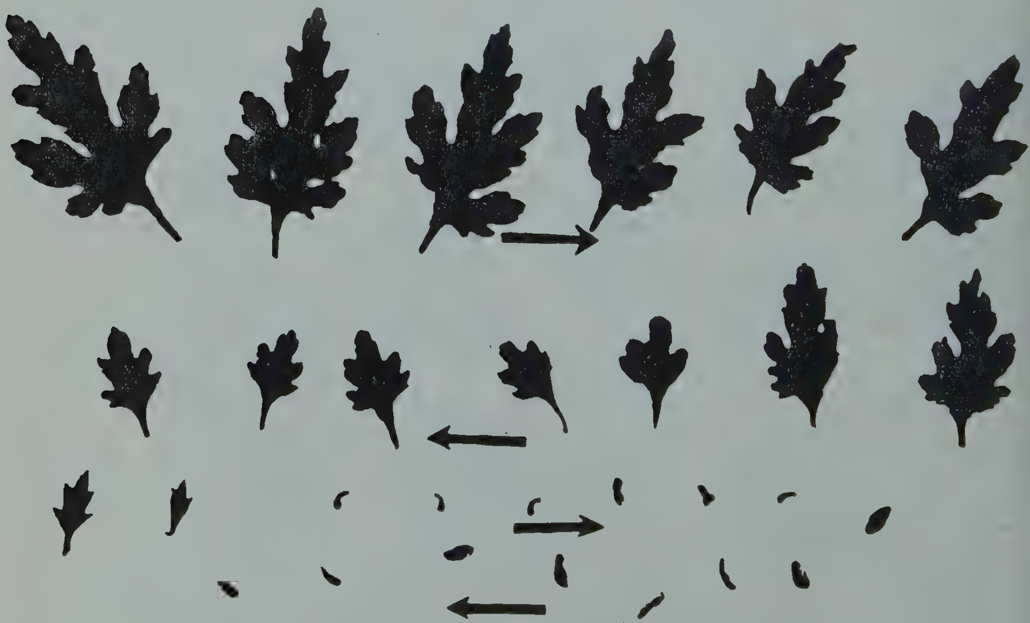
(iv) *Changes at the apex itself.* One of the most striking changes at the apex during the transition to the flowering state is the enormous increase in the size of the bare, uncommitted apex itself. From a diameter of approximately 150 μ, in the vegetative condition, the apex increases to approximately 3000 μ in diameter at the time just before floret initiation, a 399-fold increase in area. Although the apex increases gradually during growth most of this change in apical size occurs over the relatively short period of a few days.

Table 2. *Effect of gibberellic acid on flowering of vernalized and unvernalized Chrysanthemum plants*

(Variety 'Sunbeam'. Ten replicates.)

Treatment	Proportion budded	*Leaf number to budding
Unvernalized:		
0 p.p.m. gibberellic acid (control)	0/10	— (37·0)
10 p.p.m. gibberellic acid (2 c.c.)	1/10	49 (36·8)
100 p.p.m. gibberellic acid (2 c.c.)	4/10	40·8 (35·1)
Vernalized:		
0 p.p.m. gibberellic acid (control)	10/10	26·0
10 p.p.m. gibberellic acid (2 c.c.)	10/10	26·3
100 p.p.m. gibberellic acid (2 c.c.)	10/10	27·0

* Leaf number of vegetative plants at end of experiment in parentheses.



Text-fig. 2. Transition from foliage leaves to inflorescence bracts.

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[1] Kindly donated by Dr P. W. Brian.

Simultaneously, the other well-known changes take place; the type of primordium initiated changes and after a small number of rather reduced leaves have been formed the floral bracts are produced (Text-fig. 2). At this stage there is a large and in the Chrysanthemum quite rapid rise in the order of phyllotaxis. Measured in Richards's (1951) equivalent phyllotaxis index, the index is about 2·1 for the vegetative apex, and rises by 1·8 units in the reproductive. Also the time required to initiate these inflorescence bracts is reduced very considerably. Whereas, as was seen above, vegetative plants require 2·2 and 3·2 days in the vernalized and unvernalized state respectively for the initiation of each leaf, a rough average plastochron for inflorescence bracts is approximately 9 hr. To estimate such times is not very easy technically, but fortunately the terminal and upper lateral inflorescence buds of the Chrysanthemum form a more or less linear series of development, the uppermost being the most advanced. If the top and bottom members of such a set of three successive buds on a plant are dissected and the number of primordia in them determined, then a good estimate is obtained of the number of primordia present in the intermediate bud. Dissection of this bud after a further period of 1–2 days or even hours yields an estimate of the number of primordia initiated in the interval.

In the variety 'Sunbeam' about thirty such bracts are formed. Their size, especially their thickness, becomes progressively reduced, and the 'blades' of the innermost bracts are only two cells thick, any further reduction in the radial dimension would seem impossible and under ordinary circumstances bract production then ceases abruptly and floret production commences. It is an interesting fact, which may well be associated with the great reduction of the radial dimension of these primordia, that these bracts which arise round the extreme edge of the enlarging bare apex carry no lateral bud initials in their axils at all.

C. The reproductive growing point

The actual moment when the apex is to be regarded as definitely reproductive might be defined differently according to the problem under consideration. However, in general it would seem to be most satisfactory to define it as the point when any further development of it must be reproductive, i.e. when the change has become irreversible. In the Chrysanthemum this is the moment when the apex has enlarged and the receptacle is formed. The normal sequence after this concerns only the formation and development of the florets and their ultimate functioning.

As the initiation of the florets themselves begins (i.e. primordia representing axial structures) the large bare apical area is invaded and very soon used up altogether, thus terminating the growth of the original growing point. The rate of such primordial initiation has also been estimated for the outer florets in the same manner as described above for the bracts, though, of course, with a correspondingly greater margin of error. The time for the initiation of each of these florets amounts to about 24 min. under approximately optimum greenhouse conditions. At this rate about 60 florets are formed in one day, and since the inner florets are probably formed even faster, about 3–4 days will suffice to initiate the usual 200–300 florets in the bud and conclude this phase. The equivalent phyllotaxis index at this stage is approximately 7. An apex in the process of initiating floret primordia is seen in Pl. **10**.

However, the behaviour of the growing point, even after receptacle formation, is still subject to environmental control. Of the various factors investigated it appears that the light factor is the most important—acting via the leaves and leafy bracts. Two aspects of the light factor are of importance in this respect—the duration of photoperiod and also the intensity, and in unfavourable light conditions the whole sequence of development may be completely arrested. It seems most likely that these effects are indirect, acting through modification of the auxin metabolism of the plant. There are two lines of evidence for this: (*a*) any treatment causing an increase in auxin level appears to inhibit floral development; while (*b*) treatments causing a reduction of auxin level appear to overcome the inhibition.

Very briefly the experimental evidence for this is as follows. Apices of plants forming a receptacle in long-day conditions cease to develop any further after this point has been reached, and no florets are formed; the bare receptacle ends the existence of the growing point concerned (Pl. **10**). Below it the next 3–4 lateral buds then grow out vegetatively, giving rise to new shoots which may again form abortive inflorescence buds. A further set of vegetative laterals will grow out below these buds and the cycle may be repeated again and again. Although the plant, as a whole, is thus prevented from becoming truly reproductive, the terminal growing point itself cannot revert to the vegetative condition. It appears that at the moment the receptacle is formed the main apex loses its apical dominance and unless this can be re-established after floret initiation dominance is assumed by the laterals below, which then stop further growth of the terminal apex.

Similarly plants which have reached the stage of receptacle formation in short-day conditions may be inhibited from flowering by transfer to long day, but here the stage of development reached at the time of transfer is important. The latest stage at which long-day conditions can arrest the further development is that of gynoecium formation in the marginal florets.

Although there is little positive evidence as yet which is really convincing, it does seem that in long days higher auxin levels are attained.

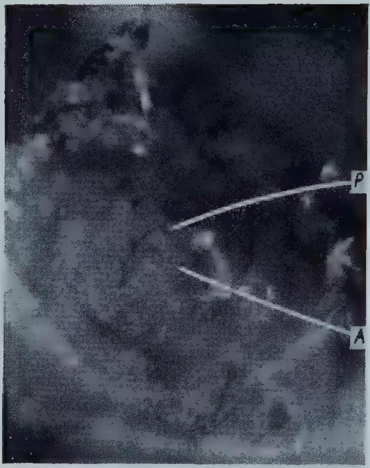
In view of this, another treatment claimed to lead to enhanced auxin effects was applied to plants which had budded in the favourable short-day conditions. This treatment which consisted in a severe reduction of light intensity (to about 25 f.c.) while the plants remained in short days, also caused the suppression of further growth of the developing inflorescence in the same way as long days, and, moreover, the same limitation of effectiveness as regards the stage of development reached at the beginning of treatment was observed. Buds which had passed this stage were not arrested.

Finally, actual application of hormones (indole-3-acetic acid in lanolin paste) just below the inflorescence bud proved to be quite as effective as long days or reduced light in stopping development, although here the effect was of course limited to the bud so treated. Once again the stage of development reached was of importance and older buds continued their development even in the presence of auxin.

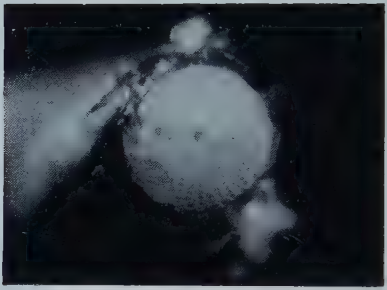
Reduction of auxin level was achieved by transfer of plants from long days to short days, which allowed the arrested inflorescence buds to recommence their development and to produce flowers, if they were still alive at this time. Also, removal of the main sources of the excess auxin produced in long days, i.e. the young vegetative laterals growing out below the bud, permitted further development of the terminal bud. This could be done either by complete disbudding of all laterals while the plant was maintained in long days, or by severing the arrested inflorescence bud itself, leaving on only a few bracts, and re-rooting it in long days. In all these instances inflorescences were produced. There was some evidence that the leaves or bracts still exerted in long days some slight inhibition, since floral development was even more rapid if the plants were transferred to short days in addition to the disbudding.

However, with these treatments some abnormalities and teratological effects became apparent. Although the development of the terminal growing point as a whole remained entirely reproductive, small parts of it produced a little vegetative growth before again ending in an inflorescence. For instance, in such inflorescences the initiation of bracts was not suddenly halted at the periphery of the receptacle, but continued until the whole of the original apex had become covered with florets. Most of such florets arose in the axils of bracts, much as in other members of the Compositae not included in the subfamily Chrysantheminae (in some Classifications) of which the Chrysanthemum is the type genus, and which is in fact characterized by the absence of such bracts.

Another such observation was the appearance of secondary inflorescences from the



(a)



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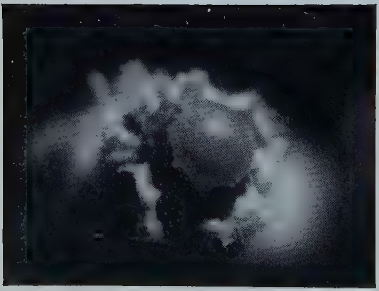

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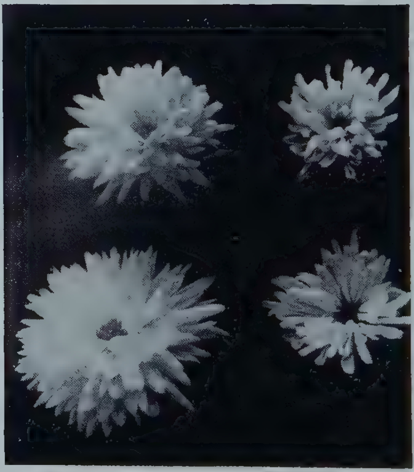

(d)

gynoecium of the marginal ligulate florets—like the hen-and-chicken daisy. A very similar effect in *Helenium*, which was recently brought to notice, was almost certainly due to accidental spraying with a hormone weed killer.

Even the individual florets may be modified in their morphology. Thus hormone treatment of the main bud frequently leads to the production of tubular instead of ligulate florets in adjacent inflorescences (Pl. **10**). Some varieties of the Chrysanthemum produce such 'quill' flowers quite normally, and it seems possible that these may differ from other varieties in their hormone levels at the susceptible stage.

In concluding this very brief survey of the morphogenetic activity of the Chrysanthemum apex, it may be said that there are two sequences of organ production: the vegetative, which is indeterminate and concerned with essentially similar structures throughout, and the reproductive, which so far as the individual apex is concerned, is determinate and is concerned with a sequence of structures showing a range of form.

Both sequences in themselves are relatively stable and can be upset by drastic treatments only, such as application of hormones or surgical techniques. The change-over from one to the other condition is itself controlled by environmental factors and in the Chrysanthemum, at least, the change-over appears possible only in one direction. Once the growing point has become reproductive it must complete this sequence or die prematurely. The actual change itself also follows a regular sequence. The great increase in apical size is associated with a related change in primordial size and possibly as a consequence their final shapes. When the radial diameter of the primordia is so small that no more bracts are produced, itself possibly a consequence of spatial factors, the bare apex is rapidly used up in the formation of the florets.

It seems likely that in the Chrysanthemum, as in other plants, the change is controlled by hormones and probably a balanced system of promotion and inhibition is concerned.

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EXPLANATION OF PLATE

Plate 10

(*a*) Bare apex (*A*) of vegetative Chrysanthemum plant after all leaf primordia have been cut away, except the youngest (*P*).

(*b*) Receptacle, formed in short day, in process of floret initiation.

(*c*) Receptacle, formed in long day, and arrested without floret formation.

(*d*) Abnormal production of tubular florets instead of ligulate florets, caused by application of indole-3-acetic acid to the plant. Left: normal inflorescences; right: inflorescences with tubular florets.

Floral morphogenesis in Primula bulleyana Forrest. By FRANK CUSICK.

Department of Botany, University of Aberdeen

(With Plate **11** and 4 Text-figures)

INTRODUCTION

In a superficial view of the inflorescence apex of *Primula bulleyana* Forrest, a central *apical dome* and a peripheral *zone of primordia* are recognizable. The primordia are those of bracts and their axillary flowers (Pl. **11**, figs. 1, 2). The youngest visible primordium, P_1, in the terminology of M. & R. Snow (1931), is in fact the tip of a bract; the inner margin of the bract becomes precisely defined only with the appearance of the axillary flower primordium, and this usually occurs when the bract is in its 4th, 5th or 6th plastochrone. The relative sizes of inflorescence apex and lateral organs are such that, for eight or more plastochrones, bract primordia or their flowers are contiguous with the margin of the apical dome. As the flower primordia (and to a lesser extent the bracts in their earlier plastochrones) present a convex surface to the apical dome, there are between existing lateral members salients of apical tissue which are the sites of future primordia. Approximately five such positions (I_1–I_5 in the terminology of M. & R. Snow) can be recognized although there is as yet no sign of independent growth at these places. Now the distinction between P_1 and I_1, based as it is on differential growth, is a real one; yet it is clearly insufficient to assign, without further examination, I_1 and its immediate successors to the inflorescence apex: they may already have their own characteristic organization, although this is not apparent histologically. With 'higher' phyllotactic systems such as the inflorescence of *P. bulleyana*, the displacement type of experiment used with success by M. and R. Snow (1931, 1933), and Wardlaw (1949, 1949*a*) is difficult to apply. Instead an attempt has been made to find out how on the apical dome the future primordia are delimited. In the method adopted, the centre of the apex is marked with a minute speck of lanoline (some 5μ in diameter); more specks are then applied, as far as possible in a radiate pattern, and their positions are recorded, as the inflorescence develops, by means of camera-lucida drawings (Text-fig. 1, A, B).

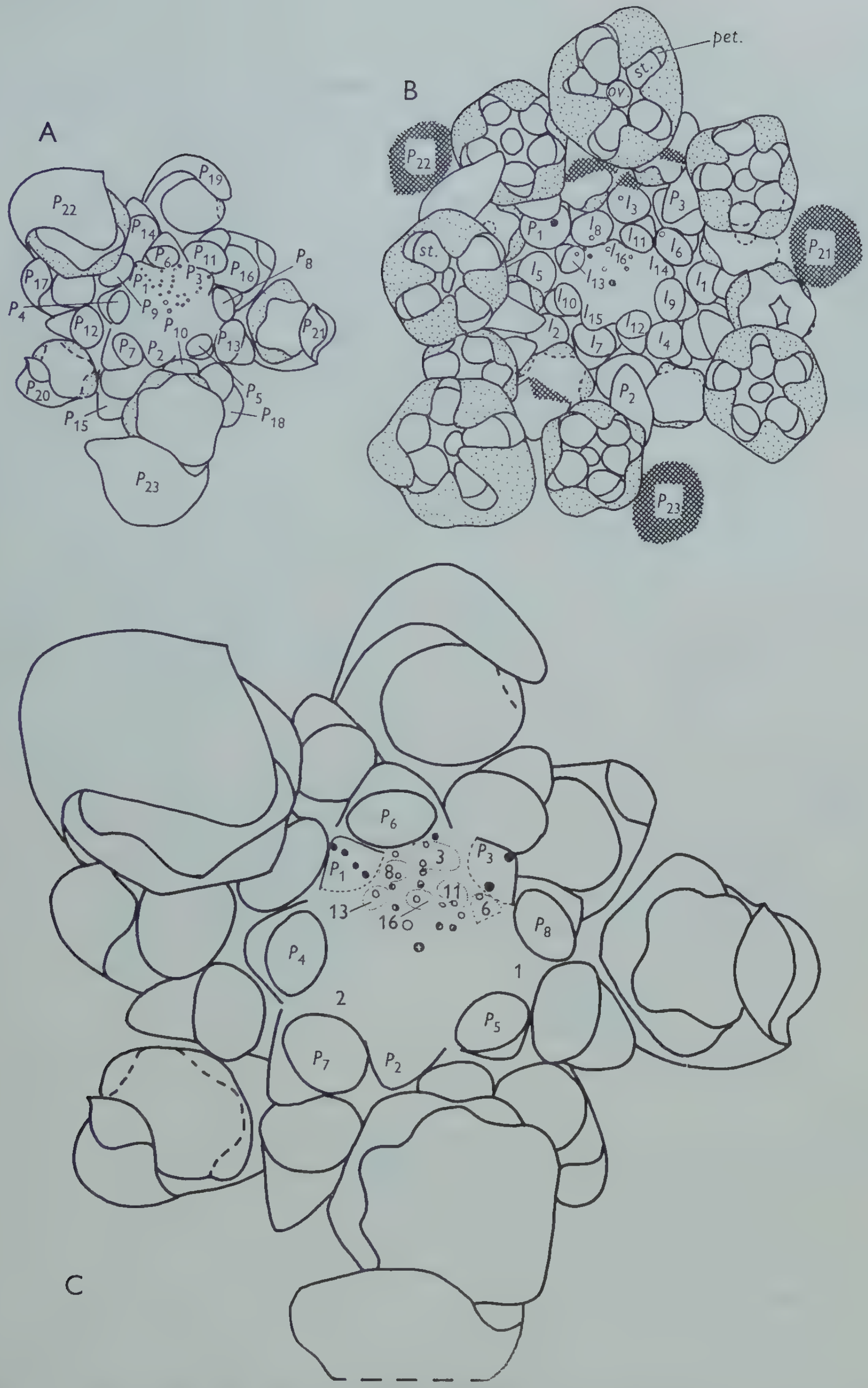
Results have not so far had the uniformity necessary for a detailed assessment of the distribution of growth throughout the apical dome, an assessment which would give direct information on the formation and activity of new growth centres. Nevertheless, the demarcation of the areas which will later give rise to particular primordia (Text-fig. 1C) is the preliminary to another method of attack—with knives. The observations are also of value in the study of phyllotaxis by means of divergence angles and provide data for the calculation of plastochrone ratios (Richards, 1948, 1951).

ISOLATION EXPERIMENTS

The presumptive positions of future primordia have been isolated from the summit of the inflorescence apex by incisions adaxial to the tissue concerned sometimes supplemented by further incisions isolating the site from existing bracts and flowers. One I_5 position, two out of three I_4 positions, one I_2 (illustrated in Text-fig. 2) and two I_1 positions survived this treatment and later formed the normal association of bract and flower. Another isolation of I_1 resulted in bract and flower developing to one side of the wound, but partly abaxial to it.

Tangential incisions were also made adaxial to the presumptive positions of eight flower primordia whose bracts were in their first, second or third plastochrones. Five of these positions developed flowers; in the other three, the bracts also failed to grow.

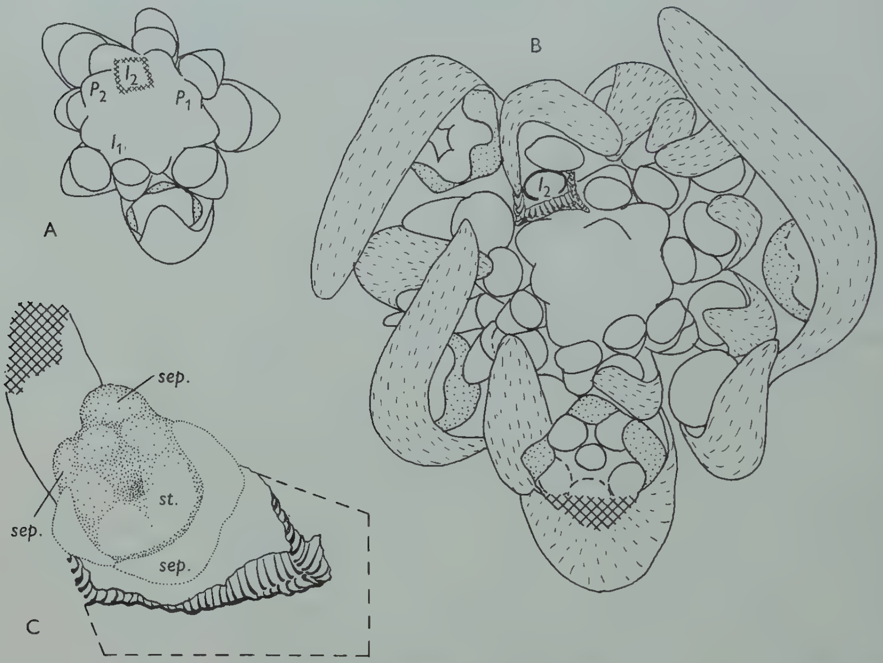
The material used in the experiments summarized above was fixed some 3–6 weeks



Text-fig. 1. Camera-lucida drawings of a young inflorescence of *Primula bulleyana*. A, the inflorescence apex newly exposed and upper quadrant marked with specks of lanoline; P_4 is the youngest bract to subtend a flower; sepals, where present, lightly stippled. (×46.) B, the same inflorescence after 12 days, showing the distribution of some of the lanoline specks. The three oldest flowers, which were arched over the centre of the inflorescence, have been removed; their cut bases, and the cut surfaces of some of the bracts, are cross-hatched; new bracts and flowers are labelled $I_1 \ldots I_{16}$; *st.*, stamens; *pet.*, petals; *ov.*, ovary. (×46.) *C*, the inflorescence redrawn (×115) from A. The boundaries of the *I* positions in the upper quadrant are inserted and numbered from data collected over a period of 13 days.

after the operations; by this time, most of the isolate flowers had reached the primordial-stamen stage. Flowers of similar age, situated on undamaged parts of the perimeter of the apical dome, served as controls. Isolates and controls showed little difference in size and stage of development.

In a comparable set of experiments, a tangential cut of greater length was made (see Text-fig. 3); it isolated a sector of the inflorescence apex which included P_3 and just excluded P_4. This sector includes I_3 and I_8, part or all of I_{11} and parts of I_{13} and I_{16}. Of nine inflorescences treated thus, four developed a bract and a flower in the I_3 position, another began similarly but the primordia later died; in another, the tissue alongside the wound hypertrophied and, perhaps because of this, I_3 developed a bract but no flower. The remaining three inflorescences showed no signs of growth at I_3. In none of the inflorescences, it will be noted, did organs form at the sites I_8, I_{11}, I_{13} and I_{16}.

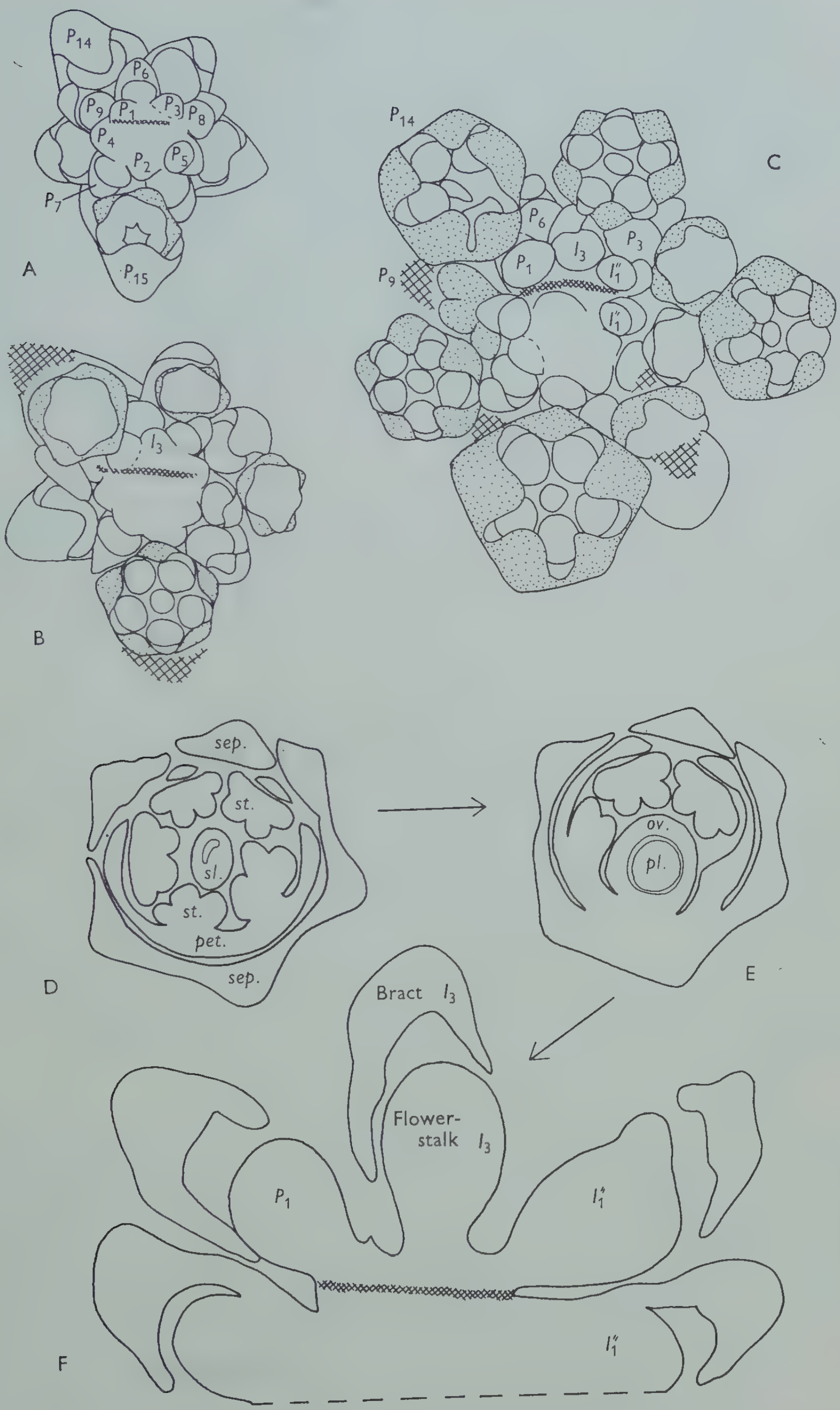


Text-fig. 2. The isolation of I_2. A and B, camera-lucida drawings at the time of isolation and after 16 days; incisions cross-hatched; sepals stippled; bracts flecked. (× 45.) C, drawings from serial sections of the bract and flower which developed from the same isolated I_2 position; material fixed six weeks after start of experiment. *sep.*, sepals; *st.*, stamen primordia. (× 90.)

As a variation of this experiment, a similar long incision has been supplemented by the puncture of P_1 and, in three of the four inflorescences used, I_3 also. Organ formation took place in two of the isolated sectors, but was difficult to analyse. One flower, apparently, was partly derived from tissue normally forming I_8; this flower had two ventrolateral bracts instead of the usual median one. The experiment will be repeated.

A further attempt to induce growth from an isolated I_8 was made by separating a larger part of the inflorescence apex. The isolated sector here included P_3 and P_4 (or most of these primordia) and also I_{11}, I_{13} and I_{16}. In three out of the four plants so treated, the isolated sector continued to develop as an inflorescence apex and soon formed normal lateral organs above (alongside) the wound.

These experiments, although they involve only a small number of replicates, leave little doubt that I_3 and older sites, when isolated from the inflorescence apex, undergo



Text-fig. 3. Isolation of a sector containing I_3 and I_8. A, immediately after incision; B, after 7 days, I_3 developing; C, after 16 days: I_3 now shows bract and flower (I_1, split by cut, is developing as two twin flowers. P_9, P_{10} and P_{14}, also damaged by the cut, are abnormal). D, E, F, drawings from serial sections of same inflorescence, fixed 6 weeks after start of experiment. *ov.*, ovary wall; *pl.*, placenta; *st.*, style. Other symbols as in Text-fig. 1A, B. (×45.)

normal development into bract and flower; there is no evidence of the suppression of one of these by the other, or of the development of a single organ of radial symmetry. The result is, in fact, that which would be expected if the bract or bract and flower already existed as growth centres in the patch of cells designated I_3. Alternatively, an I_3 in which the growth centres of bract and flower had not yet formed might produce these organs, long associated in evolution, without any regulation by the apex of the inflorescence. Histological studies have so far failed to find anatomical evidence of growth centres on the flanks of the apical dome, but this region must show some physiological differentiation, probably in a concentric pattern. The inner margin of I_3 is clearly in a different environment to the outer margin. It might be added that, although bract and flower are vastly different structures in the eyes of a morphologist or phylogenist, the differences between a bract and a sepal are not so readily apparent.

So far the presumptive position I_6 and its successors have failed to grow in isolation from the summit of the inflorescence apex and there is experimental evidence that the tissue at I_{13} and I_{16} has the essential characteristic of that at the summit of the apex: it maintains itself as a centre around which bracts and flowers develop. It is therefore suggested, first, that *within a radius extending to approximately* I_{12} *the apical dome is a unitary growth centre*; secondly, that *the morphogenetic properties of this growth centre have little effect outside the radius of* I_6. It seems probable that the zone of tissue which includes I_6–I_{11} is where the inception of the growth centres of the lateral organs occurs, and where their capacity to develop as bract and flower originates. The relationship between this zone and the apical growth centre of the inflorescence is not understood.

Further experiments relating to bract and flower

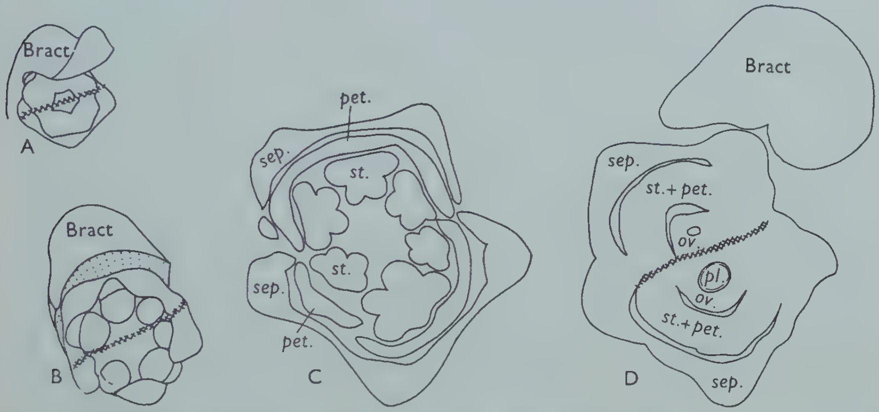
With the knowledge that the flower primordium is independent of inflorescence apex as early as I_5, it may be asked at what stage it becomes independent of its bract. The excision of the bracts of P_4 and older primordia offers no apparent handicap to their subtended flowers though these, it will be remembered, are only becoming visible at this time. No flowers have developed following excisions of P_2 and younger bracts. This may be due to faulty technique. On the other hand, the fact that in normal organogenesis in *P. bulleyana* the abaxial side of the flower grows more slowly than the adaxial side indicates some regulation by the bract. (The flowers of a foxglove, developing round an apparently similar inflorescence apex, grow more slowly on their *adaxial* side.) The morphogenetic importance of the bract primordium, therefore, is not yet to be discounted in *P. bulleyana* though many genera of angiosperms produce their flowers without bracts.

The parts of the flower

Visible stages through which the *Primula* flower passes are a *presepal stage*, a *primordial-sepal stage*, a *primordial-stamen stage*, and an *ovarial stage* (the petals appearing more or less simultaneously with the rudiment of the ovary). It has been shown (Cusick, 1956) that, until the close of the primordial-stamen stage, bisection of the flower brings about a duplication of the apical growth centre of the flower and, following this, organs develop between the new centres and the wound. The ability to form sepals in this position is lost about the middle of the presepal stage; by the close of the presepal stage, the ability to form stamens and petals here is also lost. A complete ovary continues to develop on either side of the wound following most bisections of primordial-sepal stage flowers and a minority of primordial-stamen stage flowers. Following bisections of ovarial-stage primordia, the ovarial wall grows on as two arcs of tissue separated by the wound.

In the experiments already reported, the bisecting cut was made in the median plane of the flower. It is more difficult to strike the morphogenetic centre of the flower by means of a tangential cut, and adjacent primordia are often damaged. Nevertheless, results have been obtained from this variation in procedure and they are essentially similar to those obtained from median bisections; two are illustrated in Text-fig. 4 and Pl. **11**, fig. 3.

The patterns of regeneration at the edge of the wound in bisected flowers show that stamens and petals are not local inductions by the already existing sepals; similarly, ovary wall can form without the immediate proximity of the other floral parts. It is still possible, however, that an earlier morphogenetic phase—such as sepal formation—is a necessary precursor to a later one. Stamens and corolla have yet to appear in isolation from each other. The relationship between these organs in *Primula* has long been considered, on ontogenetic evidence, to be unusually close (Duchartre, 1884); Brieger (1935), who recorded interesting abnormalities in flowers of *P. sinensis* Sabine and *P. kewensis* Hort., suggested that petals plus stamens might be induced by the action of a specific 'hormone'.



Text-fig. 4. Tangential bisection of a primordial-sepal stage flower primordium. A and B, camera-lucida drawings (× 45), A, at time of incision, B, after 8 days. C and D, drawings from serial sections of the inflorescence, fixed 4 weeks after start of experiment; *ov.*, ovary wall; *pl.*, placenta; *pet.*, petals; *sep.*, sepals; *st.*, stamens. (× 40.)

The role of the apex of the flower is scarcely tested by these bisections because apical tissue does persist on either side of the wound. The complete excision of this tissue, judged by the failure of the flower to produce an ovary, has been attempted with large numbers of primordia. A full account will be published elsewhere. It is of interest to mention, however, that by the beginning of the primordial-sepal stage (and possibly before this) sepals and stamens and petals *can* form in the absence of the floral apex. If, therefore, the apex of the flower is concerned with the formation and localization of the metabolites associated with stamen formation, it is at an early stage in the independent life of the flower. That the assembly of these staminal 'morphogens' takes place during, and is restricted to, an early phase of floral ontogeny has already been inferred from the bisection experiments: it will be remembered that by the beginning of the primordial-sepal stage stamens are no longer developed alongside the wound. After the appearance of the sepals, the organ-forming activity of the floral apex is limited to the gynaeceum.

It seems, therefore, that the answers to problems of floral morphogenesis must be sought in meristems of very small size and comparatively small numbers of cells. For this task the present techniques are crude; but it is eyestrain, not technique, which regulates the rate of progress. Reward is in seeing a plant so obviously and so beautifully alive. If a scientific reconstruction of floral development had the same sparkle, there would be cause for satisfaction.

ACKNOWLEDGEMENTS

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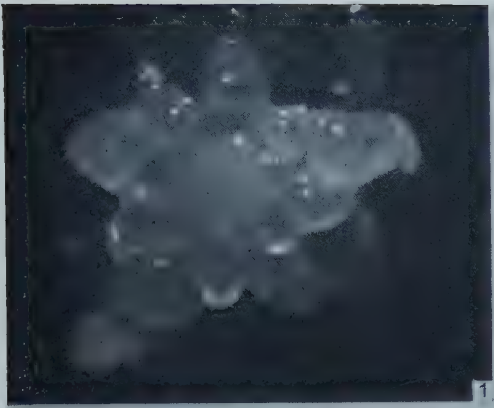
EXPLANATION OF PLATE 11

Fig. 1. A young inflorescence of *Primula bulleyana*, photographed immediately after dissection. Eighteen bracts are present in an anti-clockwise ontogenetic spiral (the oldest, bottom left). All except the four youngest bracts subtend flowers. The two oldest flowers are in the primordial-sepal stage; the rest are in the presepal stage. (× 50.)

Fig. 2. The same inflorescence photographed 18 days later. Thirty-five bract primordia are now present but the older ones are cut back and cannot be seen. All bracts except the five youngest subtend flowers. The three oldest flowers already show a distinct ovary wall and petals (which appear after the stamens in *Primula*); the next seven flowers are in the primordial-stamen stage; then follow five primordial-sepal stage and fifteen presepal stage flowers. (× 50.)

Fig. 3. This shows, on the left of the inflorescence axis, a pedicel bearing twin flowers which have resulted from the tangential bisection of the flower when it was in the presepal stage. Only calyx and corolla show in this profile but a dissection gave the following details: one twin had rings of six sepals, seven petals, and six stamens; the other had an incomplete ring of seven sepals and rings of seven petals and seven stamens. Each twin possessed a fully developed ovary. (× 1·5.)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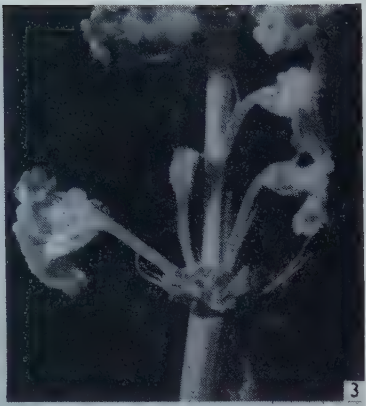
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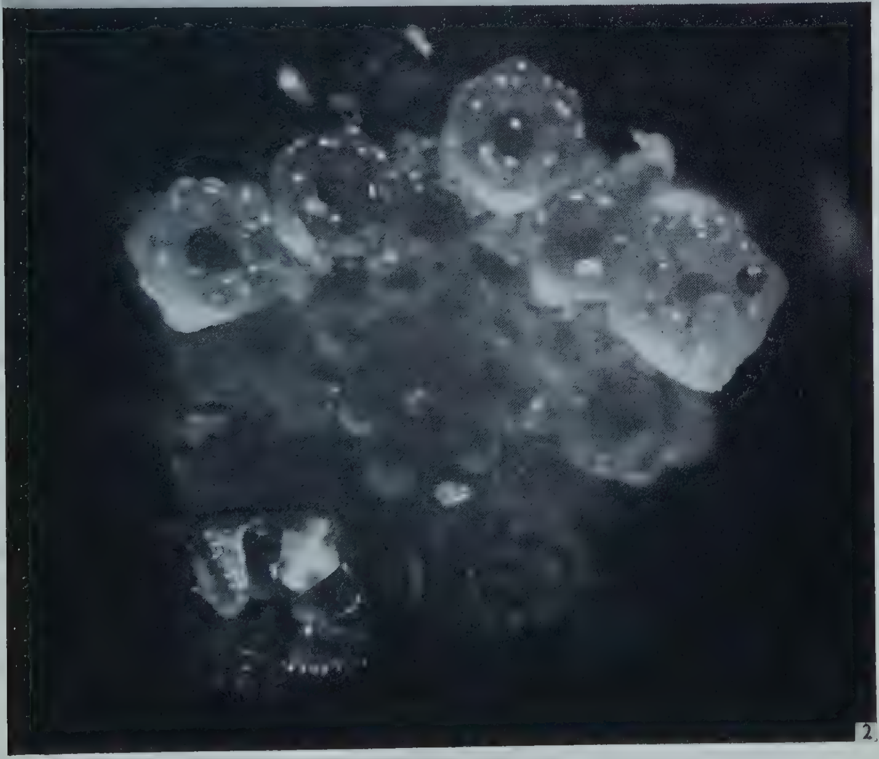
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Growth substances and flower morphogenesis. By J. Heslop-Harrison.

Department of Botany, Queen's University, Belfast

(With plates **12** and **13** and 2 Text-figures)

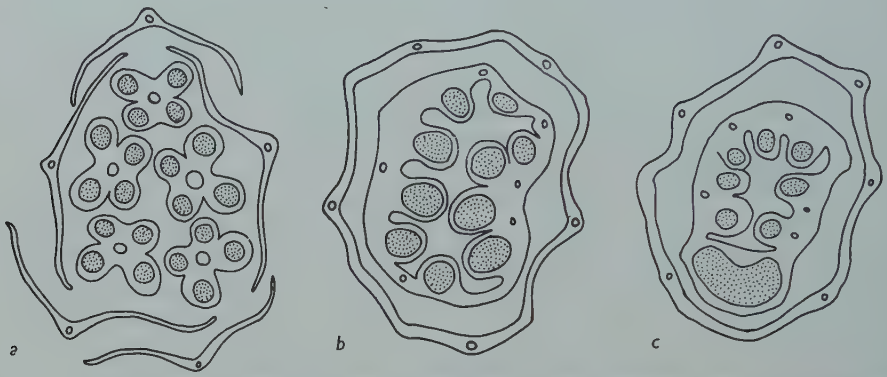
Introduction

It has long been the view of morphologists that the angiosperm flower is to be interpreted as a system composed of an axis and determinate lateral members comparable in its organization with a vegetative shoot. Those who have dissociated themselves from this view have done so partly because of difficulties in reconciling it with anatomical, ontogenetic and other peculiarities observable in certain flower types, notably those with inferior ovaries, and partly because of a revulsion against ill-considered attempts to give some form of evolutionary significance to the conception of the flower as a modified vegetative shoot. Yet leaves and the parts of flowers, in their inception, determinate growth and relationship to the axis, can justifiably be regarded as organs of the same structural category, and from the physiological viewpoint a good enough case can be made out for the classical interpretation of the flower. The evidence cautioning us against its unquestioned acceptance comes not from phylogenetical sources, but from histological studies which have been interpreted as indicating that the cell lineages which give rise to vegetative organs are not those which produce the essential parts of flowers (e.g. Buvat, 1955; see the discussion of Wardlaw, 1957*a*). We need pay little attention to any Weismannian overtones this suggestion may carry, for the capacity shown by some species to regenerate buds from leaves or leaf fragments in suitable conditions indicates clearly enough that some of the cells of leaves remain at a diploid level and are capable of entering into the organization of whole new plants; it cannot thus be true that 'vegetative' and 'reproductive' tissues are sharply differentiated genetically. Nevertheless, it could be that so far as extra-nuclear determinants are concerned the inner and outer parts of the apical meristem do indeed become differentiated from each other early in ontogeny; if so, a reappraisal of contemporary ideas about events accompanying the initiation of flowering may become due.

Whilst this issue is undoubtedly relevant to the topic of this paper, the histological facts are by no means clear (Gifford, 1954; Gifford & Wetmore 1957). I therefore propose here to join Wardlaw (1957*b*) in accepting that all appendages of the axis, from cotyledons to carpels, are products of the same 'reaction system'. On this basis, floral morphogenesis can be regarded as passing through three phases: the production at the apex of the primordia of the lateral members, the subsequent commitment of these primordia to particular developmental paths, and finally their differentiation into organs of characteristic structure and function. Whether or not these activities are truly dissociable from each other as processes, it certainly seems conducive to clear thinking to consider them separately.

Flower geometry

In the hands of systematists, all types of flowers have been found susceptible to analysis into terms of perianth members (petals and sepals, or tepals), stamens and carpels, including those in which there is concrescence to varying degrees of organs of the same or different whorls. The data of systematics thus indicate that variation in the numbers, disposition and degree of fusion of floral organs can proceed without disturbing the processes which determine the nature of those of different whorls, or their characteristic sequence. The facts of ontogeny point also to a separation in time, for the meristic, phyllotactic and other geometrical properties of flowers are established by the numbers and distributions of outgrowths on the flanks of the apical meristem, outgrowths which only later differentiate into the floral parts. These considerations lead us to expect that operative procedures aimed at modifying the geometry of apices about to form flowers will, in general, be without effect upon the nature of lateral members, or effective only to the extent that they modify consequentially the distribution of nutrients, or of determinative substances, at that critical period when the developmental fate of the laterals is being established. This presumption is borne out by findings such as those of Cusick (1957), who concludes from the results of operations upon developing flower primordia of *Primula* that the *sites* of new organs are defined by existing ones, or by the creation experimentally of new areas marginal to a new morphogenetic centre, but the *nature* of the organs formed is more a response to the morphogenetic state of the primordium as a whole.



Text-fig. 1. Modified male flowers of *Cannabis sativa* arising after treatment with 2,3,5-triiodobenzoic acid. (*a*) Normal male flower in transverse section showing free stamens and tepals. (*b*), (*c*) Transverse sections of flowers from treated plants showing complete fusion of anthers and tepals. All × *c*. 70. (From J. Heslop-Harrison and Y. Heslop-Harrison, 1957*a*.)

It is evident, also, that chemical treatments which influence the distribution of growth centres in differentiating apices may modify floral geometry, but be without direct effect upon the character of floral members. I believe this to be the key to the understanding of some of the main morphogenetic effects of 2,3,5-triiodobenzoic acid (TIBA). This substance has the property of inducing toroidal growth at stem apices (Wardlaw, 1952), and in male plants of hemp it induces a concrescence of perianth members and of stamens to form flowers of a rather regular tubular form (J. Heslop-Harrison & Y. Heslop-Harrison, 1957*a*). Even in flowers of the most abnormal type, differentiation of perianth and androecium is normal, and within the limits established by the modified geometry, function is unaffected (Text-fig. 1). It seems that TIBA is here merely modifying the pattern of emergence of the lateral members without deflecting their developmental paths. It is therefore simulating the effects of the genetical changes which, in the course of evolution, have brought about such transitions as that from polypetaly to sympetaly. Such facts support the supposition that the factors governing the initiating and spatial relationship of floral members can be dissociated from those determining their character.

THE FLORAL MEMBERS: SELF- OR DEPENDENT-DIFFERENTIATION?

Once a lateral member is initiated in the flower, its possible fates are, in general, limited to becoming a sepal, petal, stamen or carpel. The ontogenetic facts are that each begins in a similar manner as an emergent group of cells, and shows growth and progressive differentiation until the attainment of the final form. Thus at some stage in the development of any primordium it becomes directed into one of the small number of available developmental paths, and it is a commonplace of flower ontogeny that this direction is in some way a function of its physical position upon the axis.

Now we could suppose that this process whereby a given lateral primordium is directed into the appropriate developmental pathway could take either of two forms. Development and differentiation towards the final structure might be autonomous after an early determining[1] event, or the ultimate form might be reached only as a result of a succession of stimuli reaching the differentiating primordium from outside itself. In epigenetic terms, the first would be an instance of self-differentiation, the developing organ requiring only the basic nutrients to complete its ordained course, and the second, one of dependent-differentiation, the organ requiring the appropriate specific morphogenetic stimuli for the successful completion of its development, as well as nutrients.

Can we decide between these alternatives? Or is neither the whole truth? We may take as a first line of evidence what is already known for vascular cryptogams. Operative techniques such as those used by Wardlaw and his colleagues (Wardlaw, 1949; Cutter, 1957), and culture experiments, especially those of Wetmore's school, have indicated what might reasonably be suspected to represent a general pattern of differentiation for the lateral organs of vascular plants. Primordia pass through an early phase of lability, after which they become determined and capable of self-differentiation to a final characteristic form. This has been elegantly demonstrated for leaves of the fern, *Osmunda cinnamomea* L. (Wetmore, 1956; Steeves, 1957; Steeves & Sussex, 1957). Isolated and grown *in vitro*, the very youngest prospective leaf primordia formed structures with radial symmetry of the nature of buds and capable of growing into whole plants; those which had passed a certain age, but which were yet to undergo morphogenesis, formed normal dorsiventral leaves *in vitro*. Thus the young primordium shows a generalized property of regenerating the whole plant, whilst later it becomes restricted to one particular path of development. The extension of these findings to flowering-plant leaves seems imminent (Wetmore, 1956).

So far as these findings with leaves can be applied to the flower, they would seem to indicate that determination is likely to take place in the very early growth of the lateral primordia, after which their differentiation into perianth members and essential organs proceeds autonomously.

However, it seems that this can be so only within limits. Determination probably does occur in the early growth of the primordium, but whether the normal developmental path is pursued to its end appears to be dependent upon specific influences entering the developing primordium from the axis. Two types of evidence point this way, arising (*a*) from culture experiments, and (*b*) from experiments with intact plants in which flower character has been modified in specific ways by treatments with growth substances.

(*a*) *The evidence of culture experiments*

Culture experiments with anthers (Gregory, 1940; Taylor, 1950; Lima-de-Faria, 1950; Sparrow, Pond & Kojan, 1955) have shown that in many plants, meiosis and pollen formation proceed to a normal conclusion only if the anther is taken into culture in a relatively late stage of differentiation, usually after zygotene in the meiocytes. Anthers excised before the onset of the meiotic prophase show simply a degeneration of the archesporium, or a proliferation by mitotic divisions without the normal rounding off of the meiocytes. This failure can hardly be attributed to deficiencies of major nutrients, since it occurs in media in which the later stages of pollen formation proceed normally—and indeed, as we have found with *Hemerocallis*, in which young anthers will grow freely to dimensions substantially greater than normal. Evidently the successful initiation of meiosis in the outgrowing stamen is dependent upon some stimulus passing into it over a period of time, so that it is not capable of self-differentiation to a degree comparable with the leaf primordium of *Osmunda*. The stimulus need not, of course, be a specific hormone; it may be simply that the outgrowing stamen requires a particular quantitative combination of nutrients, auxins and possibly cell division factors during its early growth for normal differentiation.[1] What is significant for the present argument is that there is sufficient evidence to show that determination is not positively accomplished in the very earliest stages of emergence of the primordium, but that the path of differentiation may be influenced in a relatively late phase by factors arising outside of the stamen itself.

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[1] The term 'determination' is used in this paper in the normal sense of animal embryologists, to refer to the fixation of the fate of a tissue in development so that it will differentiate along one particular path (cf. Needham, 1942), and not in the unusual sense of Skoog & Miller (1957), 'irreversible loss in regenerative capacities of cells and tissues'.

(*b*) *The governing effects of applied auxins*

Experiments with applied auxins show decisively that after the initiation of the primordia of perianth and essential organs in monoclinous flowers their future paths of development can be influenced in various specific ways via the floral axis. This was demonstrated by Resende (1953) with a biennial race of *Hyoscyamus niger* L. Administration of indole-3-acetic acid (IAA) by injection of the ammonium salt in aqueous solution into the stems of plants about to flower brought about specific changes in the structure of the inflorescence and flowers. The bracts showed hypertrophy, and in a proportion of flowers the outgrowth of the corolla and essential organs was suppressed, whilst the calyx grew to an abnormal size. In flowers which continued development (presumably in the presence of lower concentrations of auxin) the outgrowth of the calyx and gynoecium was promoted, and that of the androecium and corolla suppressed.

Comparable results have been obtained with the long-day annual, *Silene pendula* L. (J. Heslop-Harrison & Y. Heslop-Harrison, 1958*a*, *b*). In this case the auxin, α-naphthaleneacetic acid (NAA), was introduced into the plant through the leaves, either in aqueous solution or in a lanolin medium before and during flower differentiation. With general applications given early in life, the total flowering response was reduced, and a substantial proportion, 51·9 %, of the total number of anthers produced failed to form viable pollen. When treatment was localized to individual flowering branches, the specific effects upon flower structure became strikingly evident. In the var. *ruberrima*, practically all of the anthers produced on auxin treated branches failed to differentiate normal pollen, and their corollas were suppressed to a greater or lesser degree; in contrast the calyces were abnormally inflated, and the ovaries substantially enlarged (Pl. **12***a*).

There can be little doubt about the meaning of these results. In the development of monoclinous flowers like those of *Hyoscyamus* and *Silene* the primordia of sepals, petals, stamens and carpels are formed in serial order and their prospective fates determined. But whilst their potentialities are thus established, the degree to which these are realized depends upon stimuli received during their growth and differentiation. In particular, it seems that auxin levels in the developing flower assume importance at this time, the growth optima of sepals and carpels lying at a higher level than that of petals and stamens (Heslop-Harrison, 1957*a*, *b*). An upward shift in auxin supply thus checks the normal growth and differentiation of corolla and androecium, even to the extent of almost total suppression, while simultaneously driving that of calyx and gynoecium beyond the stage at which it would normally cease. It is worth noting that this promotion of calyx and gynoecium does involve differentiation beyond the normal and not merely growth sustained over a longer period; thus the enlarged sepals may become foliaceous, and the ovary may pass beyond the condition of the normal flower at anthesis and develop immediately the special characteristics which normally await the accomplishment of pollination—that is to say, it may differentiate directly into a fruit (J. Heslop-Harrison & Y. Heslop-Harrison 1958*a*).

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[1] In the most recent work on anther culture with *Allium cepa* L. (Vasil, 1957) there is a clear indication that self-differentiation will proceed in anthers excised before synapsis in culture media supplemented with kinetin and gibberellic acid, but in anthers excised in stages earlier than leptotene meiosis is not initiated.

Auxin effects in monoclinous flowers

The striking feature about these effects of auxins in genera with basically hermaphrodite flowers like *Hyoscyamus* and *Silene* is that they do not concern the fundamental architecture of the flower, nor yet do they clearly involve a deflexion of the developmental paths of its lateral members. A flower of *Silene* rendered functionally female by auxin treatments carries staminal rudiments, as in a genetically female plant of *Melandrium*. And no treatment has yet been found which will deflect the development of a stamen primordium in *Silene* so that it assumes even a suspicion of a carpelloid form. Manipulation of the auxin supply may thus be said to affect flower structure in these genera merely by hastening or retarding the progress of the different floral members along their characteristic developmental paths. It seems that auxin is here acting as a regulating rather than as a determining agent. What in fact determines the prospective fate of the different classes of primordia in the monoclinous flower remains to be established. It cannot be without significance that the zonation of the flower members follows a standard order—calyx, corolla, androecium and gynoecium—which experimental treatments have so far failed to upset in any systematic way. In the basically hermaphrodite flower this obligate sequence of organs seems rather too rigid to be a straightforward case of physiological correlation based upon a gradient system. Perhaps the determination of the whorls of lateral members in a flowering apex successively in space and time is brought about by a relay-like action, the onset of each phase being conditional upon the completion of the previous, and leading inevitably to the initiation of the next (cf. Cusick, 1957; Wardlaw, 1957*b*).

I believe this point is illustrated in another way by the systems of zonation of sex function observable in monoecious, gynomonoecious and andromonoecious representatives of families with basically hermaphrodite flowers (Heslop-Harrison, 1957*a*). In these there is almost invariably a graded variation in the relative development of gynoecium and androecium, the gradient being referable either spatially to the proximal apex, or temporally to the order of formation of flower primordia (Correns, 1928). These gradients can be modified experimentally (e.g. with *Cleome spinosa* (Murneek, 1927), and *Musa paradisiaca* (Joshi, 1939)), and the sex function of flowers affected accordingly. It seems probable that graded variation in the relative development of androecium and gynoecium in monoclinous flowers is governed by auxin gradients in the inflorescence axis, and that it is this that experimental treatments affect. In our experiments with *Silene pendula* this sort of effect has, in fact, been obtained. Flowers developing in the neighbourhood of the sites of auxin administration show the most pronounced suppression of the androecium and the most enlarged gynoecium; those developing later in more remote parts of the inflorescence regress to a more normal balance.

But the essential point is that in these graded systems of sex function the basic architecture of the flower does not change; the males bear gynoecial rudiments, and the females, androecial. It is not the character or sequence of the organs produced in the different flowers which is affected, but their relative development.

Auxin effects in basically unisexual flowers

Some of the most convincing demonstrations of auxin effects upon flower character during recent years have concerned species with what I have termed basically unisexual flowers. These are species in which the flower gives no evidence of recent derivation from a hermaphrodite form—unlike, for example, dioecious *Melandrium*, in which the architecture is quite clearly based upon a hermaphrodite plan. This distinction has been criticized (Parkin, 1957), but the facts of floral morphogenesis require that we should retain it in the present state of knowledge (Heslop-Harrison, 1958).

(*a*) *The monoecious cucurbits*

In the Cucurbitaceae, a family with no hermaphrodite genera, there is evidence that the character of floral primordia, whether they shall form pistillate or staminate flowers, may be affected by auxin treatments. In *Cucumis sativus* L., the proportion of morphologically female flowers formed at early nodes may be substantially increased by spraying plants after the unfolding of the first foliage leaf with aqueous solution of IAA and NAA at 0·1 % (Laibach & Kribben, 1950*a*, *b*). In *Cucurbita pepo* L., where one flower is normally produced at each node, the node at which the first female is formed may be greatly advanced by auxin treatment under conditions of day-length and night temperature which would normally delay the appearance of flowers of that sex (Nitsch, Kurtz, Liverman & Went, 1952; Heslop-Harrison, 1957*b*). Substantially the same effects may be produced in the cucurbits by exposure to atmospheres containing small percentages of unsaturated carbon gases.[1] Minina (1938, 1952) and Minina & Tylkina (1947) observed that treatments for periods of 11–12 hr. with atmospheres containing carbon monoxide concentrations between 0·1 and 1 % results in marked deviations from the normal ratios of male and female flowers produced by *Cucumis sativa*. The effect is consistently in the same direction: to reduce the proportion of male flowers, even to the extent that female flowers are formed exclusively. The female flowers produced as a result of this treatment are functionally normal, but the fertility of those males appearing in the immediate post-treatment period may be substantially reduced. Ethylene is effective in promoting this female sexualization in cucumber at lower concentrations than carbon monoxide, a result in accordance with what is known concerning the relative effectiveness of the two gases in other auxin-simulating activities (Zimmerman & Hitchcock, 1933). Apart from influencing the ontogeny of the essential organs of the flower, the unsaturated carbon gases affect also the perianth members (Minina, 1952). In the cucumber, the sepals of both male and female flowers show hypertrophy after brief exposure to atmospheres containing low percentages of carbon monoxide, whilst the corolla is severely reduced, and may even fail to expand at all. Identical symptoms arise in *Cucurbita pepo* following NAA treatment (Pl. **12** *b*, *c*), and the parallel with the reactions of *Hyoscyamus* and *Silene* is obvious.

At first sight there would seem to be little reason to doubt that in these experiments with the cucurbits, female flowers do indeed occupy sites which would otherwise carry males. This would mean a conversion of one type of primordium into another, and would carry the implication that in this context applied auxins can act as determinants. But it is still possible to argue that what is involved is the activation or inactivation of primordia of two different classes on condensed axillary racemes. We have obtained evidence that might support this contention from *Echinocystis*, a cucurbit in which a solitary female flower and a raceme of males are formed at each flowering axil. Treatment with NAA in the seedling stage checks the development of the males and promotes that of the females at successive nodes of the main stem. The effect here is patently upon the relative growth rates of two types of flower primordia, much as in the case of stamens and carpels in auxin treated hermaphrodite flowers. It is also noteworthy that auxin treatment of cucurbits does *not* result in intersexuality or sex reversal in male flowers; stamens are not converted into carpelloid structures by deflexion from their normal developmental path, nor indeed, do gynoecial structures appear in the centre of staminate flowers. On the other hand, male flowers may be rendered sterile by auxin treatment in the cucurbits (Nitsch, Kurtz, Liverman & Went, 1952; Pl. **12**c).

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[1] That the unsaturated carbon gases in low concentrations may produce effects in plants simulating those resulting from auxin sprays has been known since the work of Zimmerman, Crocker & Hitchcock (1933*a*, *b*). Responses to concentrations of carbon monoxide of the order of 1 % include leaf epinasty, abnormal stem extension and the formation of adventitious roots on aerial parts.

(b) *The dioecious* Cannabis sativa

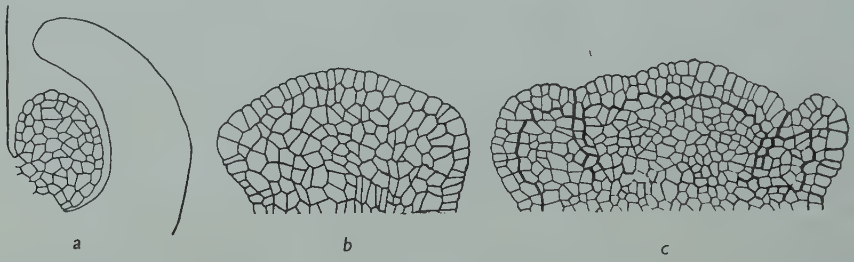
There is thus room for doubt as to whether experiments with the cucurbits do in fact show that auxins may assume the role of determinants so far as the fate of flower primordia is concerned. With the dioecious *Cannabis sativa* L., however, there seems no question about the fact that auxin-induced intersexuality and sex reversal in genetically male plants arises from a diversion of the ontogeny of presumptive stamens from their normal path towards that characteristic of carpels. With NAA treatment in the period immediately preceding the differentiation of flowers, male plants can be made to pass through a phase in which female flowers are produced (Heslop-Harrison, 1956) before reversion to their genetical sex, and the female flowers occupy the sites which would otherwise carry males.

Moreover, in induced intersexes of hemp, types of sporophyll may appear which are intermediate, ranging from those which are normal stamens with stigmatic tips to those which are carpels in all respects except that they bear one or more pollen-sacs (Pl. **13** *d–f*). There is thus no doubt that any one floral member is free to assume either developmental path, and that if it is not committed positively to one or other as a primordium it may differentiate so as to produce structures of intermediate character.

A striking feature of intersexuality and sex reversal in male plants of hemp, whether the causal agent be chemical or a physical factor of the environment, is that there is a relatively rapid return to the normal genetical sex in flowers formed after the withdrawal of the modifying agent, and even sometimes before this. It seems that the genetical determining system is in some degree buffered, allowing relatively rapid compensatory regulation. This is especially true of auxin-induced sex inversion. Single doses of NAA will produce the characteristic effect only when supplied at the onset of a flowering period, and the effect is observable for only a limited number of flowering nodes. This fact presumably means that only those flower primordia which pass through a phase of competence during the critical period when auxin levels in their neighbourhood are abnormally high are likely to differentiate carpels in lieu of stamens.

The difficulties of achieving a controlled and localized introduction of auxins such as NAA into plants almost prohibit study of their effects on flower morphogenesis except in the most general way, but the unsaturated carbon gases form a tool which is slightly less blunt in that their action can be controlled more satisfactorily in time. As with the cucurbits, carbon monoxide simulates the effects of auxins in hemp, and a single treatment of 48 hr. with a concentration of 1% carbon monoxide given early in a phase of flower differentiation following photoperiodic induction is sufficient to cause intersexuality at several successive flowering nodes. Since the male inflorescence of hemp shows a very regular acropetal flowering sequence, it is possible to establish the probable state of successive primordia at the beginning of a 48 hr. treatment period and so, within fairly broad limits, to determine the range of primordia competent to react by a modification of subsequent ontogeny (J. Heslop-Harrison & Y. Heslop-Harrison, 1957*b*). Judging from the behaviour of the basal flower primordia in axillary inflorescences, it seems that those which are showing the earliest signs of emerging laterals, being in longitudinal section slightly flattened above (Text-fig. 2*b*), are likely to react. Those at a younger stage, simple domed meristems with no indications of laterals (Text-fig. 2*a*), are not diverted in ontogeny by single treatments. In flower primordia of the size of those in Text-fig. 2*c*, the fate of the lateral members is probably determined, and their differentiation will proceed along the normal path whether or not they receive carbon monoxide treatment.

These results suggest a situation in hemp analogous with that, discussed above, established for fern leaves by the Harvard school. The lateral members of the flower seem to arise as uncommitted growth centres; these pass through a period of competence during which they will normally undergo determination, their fate subsequently being to differentiate into an organ of particular character. Unfortunately it is quite impracticable to demonstrate this by organ culture techniques of the kind adopted for fern leaves; the flowers of hemp are very much too small for this type of manipulation. However, an approach has been made to the same end by apex grafting experiments (J. Heslop-Harrison & Y. Heslop-Harrison, 1957*b*). Apices carrying flower primordia in the very earliest phases of differentiation were exposed to a single carbon monoxide treatment and then grafted on to untreated plants of the same age and sex. During subsequent flowering, the grafted apices proceeded to develop intersexual flowers in sites where these might have been expected had the transfer to an untreated plant not taken place. This indicates clearly enough that some form of determination takes place during the period of treatment, after which the floral members undergo self-differentiation. The alternative possibility, that the modified ontogeny is guided by a continuing stimulus from the vegetative parts of the plant, seems to be ruled out.



Text-fig. 2. Flower primordia of male plants of *Cannabis sativa*. (*a*) Primordia of this size are unlikely to respond to a single brief exposure to 1 % CO by a later modification in ontogeny. (*b*) Primordia at this stage may respond to CO treatment. (*c*) Primordia of this size are determined, and cannot be modified in subsequent ontogeny by CO treatment. All × 240. (From J. Heslop-Harrison & Y. Heslop-Harrison, 1957*b*.)

If this interpretation of the course of events in the early development of the hemp flower is correct, then it must be accepted that the determination of the floral members can be influenced by auxins and by agents such as carbon monoxide which simulate auxins. The effect of raising auxin levels appears to be to divert the ontogeny of presumptive stamens towards that characteristic of carpels. It may be noted that the converse effect, the modification of sexuality in female plants by chemical treatments lowering the levels of native auxins, is yet to be demonstrated. Environmental conditions are known in which female plants of some hemp strains show sex reversal (Borthwick & Scully, 1954), but whether this is a result of modified auxin metabolism remains to be demonstrated.

The different classes of auxin effects

Plant morphologists have been accused of a predilection for cleaving trichomes; it may seem that I am similarly culpable in pressing the distinctions which I have sought to make in the preceding paragraphs. Yet I believe they should be made at this stage. In all the examples mentioned, the effect of supplying endogenous auxin is, from the functional viewpoint, to shift the balance of sex expression in whole plant or individual flower towards 'femaleness' and away from 'maleness'; but looked at from the morphological point of view, the means by which this is achieved seem on the face of it somewhat different. Three situations can be recognized, which may be summarized as follows.

(*a*) In species with monoclinous flowers, auxin treatment given in the early phases of flower differentiation may alter the balance of growth of the various floral members, suppressing the development of androecium and corolla, and promoting that of gynoecium and calyx. In no experiment has it been shown that applied auxins may deflect the developmental path of stamens so as to produce carpelloid organs, nor modify the basic architecture of the flower in any other way than that just stated.

(*b*) In *Echinocystis* and possibly other monoecious cucurbits the administration of auxin during flower differentiation suppresses the development of putative male flower primordia whilst promoting that of females. Again there is no evidence that auxin treatment can provoke intersexuality in the structures of male flowers.

(*c*) In male plants of dioecious hemp, auxin treatment in the early-flowering stages affects the determination of stamens, causing a partial or complete conversion into carpels. Concomitant changes in the corolla suggest that here, too, there is a re-direction into a developmental path closer to that in flowers of genetically female plants.

In situation (*c*), it seems that auxin is participating in some determining process in the flower. In (*a*) and (*b*) there is no reason yet to suspect this; rather does it seem that the auxin metabolism during the flowering period may act primarily as a regulating system, governing the relative developmental rates of primordia already determined by other, unknown factors.

Environmental influence and flower character

It follows from the foregoing that environmental factors influencing the native auxin metabolism of the plant during a flowering period may be expected to affect floral characteristics in specific and predictable ways. There is, indeed, a temptation to invert the argument, and to suppose that environmental conditions producing particular manifestations in the flower simulating those evocable by exogenous auxins necessarily do so through the agency of the endogenous auxins. While agreeing that the logic here is not above reproach, I confess to a conviction that this is so. Two years ago I reviewed the evidence concerning environmental control of flower sexuality (Heslop-Harrison, 1957*a*), and concluded that there was a consistency in the effects of several factors sufficient to indicate a common basis of action. Since that time the accrescent data have in the main served to reinforce this conclusion. The evidence that this common basis of action is indeed the auxin metabolism of the plant arises not only from the similarity of so many environmental effects upon flower structure to those induced by applied auxins, but also from parallel effects upon vegetative growth. Scarcely any other interpretation seems possible for such observations as those of Resende that the light regimes which provoke rooting in the aerial parts of succulents (Resende, 1946) are those which in the same plants lead to suppression of androecium and corolla and hypertrophy of calyx and ovary (Resende, 1950).

Another pertinent line of evidence has recently been stressed by Baker (1957): that arising from effects of parasitism upon flower morphogenesis. Perhaps the best known instance is that of dioecious species of *Melandrium*, in which attack by the Basidiomycete *Ustilago violacea* leads to the appearance of stamens in the flowers of genetically female plants. This case has long been considered a critical one for the comprehension of sex determining systems in plants (cf. Goldschmidt, 1956), and it promises to take on a new significance in the light of what is now known concerning the effects of auxins upon flower structure in hermaphrodite Caryophyllaceae such as *Silene*.

The principal morphological changes arising from *Ustilago* infection in *Melandrium album* and *M. rubrum* are well documented (Schopfer, 1940; Baker, 1947*a*, *b*). Both male and female plants may be infected, the significant flower changes occurring in the females. In them, anthers are formed and pass through an initial period of differentiation identical with that in the male flower. The pollen mother cells are invaded by the mycelium of the parasite before the onset of meiosis, and the anthers ultimately become filled with brand spores. Whilst it is this effect which has caught most attention, the concomitant changes in the female plants are almost as significant. Normally the female plant is less floriferous than the male; infection greatly enhances the numbers of flowers formed (Schopfer, 1940). Infected female flowers not only produce stamens, but also show a substantial reduction in ovary size and style length; accompanying this is a reduction in the dimensions of the calyx. If it is permissible to argue from the evidence of *Silene*, one may speculate that the common basis of all these symptoms lies in an interference by the fungus with auxin metabolism in the early flowering period in such a manner as to reduce auxin levels in the neighbourhood of differentiating primordia. Following this line of thought, we have recently been looking into the effects of infection upon enzyme activities in tissues of female plants. An enhanced level of peroxidase activity can usually be detected in extending flowering shoots compared with that in corresponding tissues of normal females. Results so far with 'IAA oxidase' prepared by the methods of Galston & Dalberg (1954) and Konishi (1954) have so far been equivocal; although differences in the activity of extracts appear, much seems to be dependent upon the photoperiodic experience of the plant.

In another example of disease-induced change in flower structure, the evidence favouring the idea that the effect is mediated through the agency of auxin is very strong. The smut *Ustilago zeae*, which infects *Zea mays* L., characteristically produces large tumours, often in the region of the inflorescences. In addition to the primary symptoms, changes occur in the terminal inflorescence, usually entirely staminate in maize. A proportion of the flowers form normal gynoecia, which may even prove fertile (Heald, 1926). As has been shown by Wolf (1952), IAA is produced as a metabolic by-product of *Ustilago zeae* cultured in the presence of tryptophane, and the formation of corn smut galls has been associated with high auxin levels in the plant (Moulton, 1942). If the monoecism of maize is governed by an auxin gradient, then the appearance of female flowers in the terminal, normally male, inflorescence might well be expected as a symptom of an infection which has as one result an elevation of the levels of free IAA in the host tissues. It is noteworthy that environmental conditions which provoke this same type of change in the flowers of the maize tassel, namely short days and cool nights (Schaffner, 1927; Richey & Sprague, 1932; Choudri & Krishan, 1946), are those which increase the proportions of female flowers in the cucurbits and bring about sex reversals in the flowers of genetically male plants of hemp. These effects in the cucurbits and hemp can be simulated by auxin treatment; it remains to be seen whether the formation of female flowers in the tassel of maize can be induced in a like manner.

SUMMARY AND CONCLUSIONS

1. From a physiological viewpoint, the classical interpretation of the flower as a system composed of an axis and determinate lateral members, comparable in its organization with a vegetative shoot, remains acceptable. On this basis, the processes of floral morphogenesis can be regarded as falling into three phases: the initiation of the lateral primordia, their commitment to particular developmental paths, and their differentiation into organs of characteristic structure and function.

2. The basic geometry of the flower is established by the activity of the apex in forming, in particular spatial relationships, growth centres which produce primordia of different prospective classes. This may be modified in experiment by operative procedures, and also by such agents as 2,3,5-triiodobenzoic acid, without affecting the processes which determine the nature of the floral organs themselves.

3. If the evidence from recent work on the behaviour of leaf primordia is accepted as relevant, it might be supposed that determination is likely to take place in the early life of the floral member, its subsequent differentiation being autonomous. The evidence of

anther culture work indicates, however, that normal differentiation does not proceed without continuing stimuli from the floral axis; there is, for example, no recorded instance of meiosis having been initiated in the archesporium of an anther taken into culture earlier than leptotene.

4. In the intact flower, major changes in structure and function may be induced by exogenously supplied auxins. These may be summarized as follows:

(*a*) In species with monoclinous flowers, corolla and androecium may be suppressed to a greater or lesser extent, whilst calyx and gynoecium undergo hypertrophy.

(*b*) In monoecious species like the cucurbits, the appearance of the first female flower may be advanced in time whilst the ratio of male to female flowers falls.

(*c*) In the dioecious hemp, male plants produce female or intersexual flowers.

5. The effects of auxins upon the development of monoclinous flowers is restricted to changing the balance of growth between floral members of different types. There is no recorded instance of a primordium of one prospective type being deflected into a foreign developmental path as a result of auxin treatment. From this it may be concluded that auxin is here likely to be acting as a regulating rather than a determining agent.

6. In the monoecious cucurbits, whilst it may be that the female flowers arising after auxin treatment do indeed occupy sites which would otherwise carry males, it is also possible that what is involved is the activation or inactivation of flower primordia of different types on greatly condensed axillary racemes. Moreover, auxin treatment of cucurbits does not result in intersexuality in male flowers, as might be expected at least occasionally were auxin acting as a determinant in the early growth of stamen primordia.

7. In the dioecious hemp, auxin-induced intersexuality and sex reversal in genetically male plants seems to arise from a diversion of the ontogeny of presumptive stamens from their normal path towards that characteristic of carpels. In this instance, auxin may be influencing some determining process in the flower primordium.

8. Since floral morphogenesis can be influenced by applied auxins, it is to be expected that environmental factors influencing auxin metabolism should affect flower structure in consequence. Whilst it does not necessarily follow from this that conditions producing structural changes simulating those evocable by auxins necessarily do so through the agency of the native auxin metabolism, there is a regularity and consistency in the effects of some environmental factors which suggests that this may be the case.

9. The effects of certain fungal infections upon floral morphogenesis provide a further pertinent line of evidence. *Ustilago zeae* infects *Zea mays*, causing, among other symptoms the formation of female flowers in the normally male terminal inflorescence. If the monoecism of maize is governed by an auxin gradient, such a result is not unexpected, since the fungus is known to produce IAA in culture in the presence of tryptophane, and the formation of the characteristic corn smut galls has been attributed to this cause. *Ustilago violacea* produces an effect of an opposite nature in its host, the dioecious *Melandrium rubrum*, stimulating the formation of stamens in flowers of genetically female plants. It might be surmised that this effect arises from a depression of auxin levels in the neighbourhood of differentiating flower primordia, but this aspect of the metabolic disturbances associated with infection is yet to be examined.

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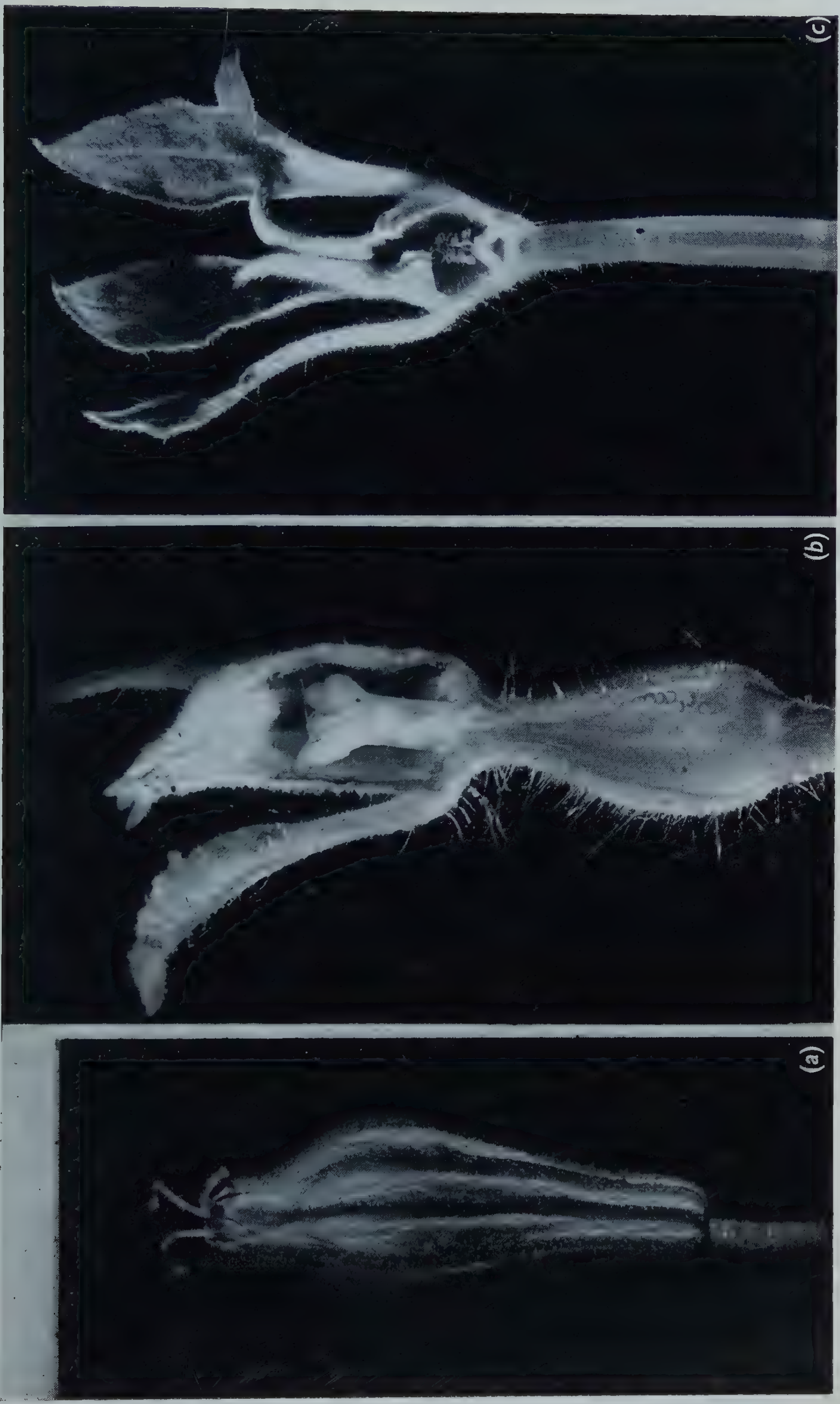

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EXPLANATION OF PLATES 12 AND 13

Auxin and CO-induced modifications of flower structure in *Silene pendula*, *Cucurbita pepo* and *Cannabis sativa*.

PLATE 12

(*a*) *Silene pendula*. Male-sterile flower from a NAA-treated branch of an otherwise fully fertile plant. Note the precocious emergence of the styles, the arrested corolla, and the inflated calyx surrounding the abnormally enlarged gynoecium. (× *c*. 6.)

(*b*) *Cucurbita pepo*. Female flower formed at an early node of a plant grown under long days following NAA-treatment in the seedling state. Note foliaceous calyx and partly suppressed corolla. (× *c*. 2·5.)

(*c*) *C. pepo*. Sterile male flower from an early node of a plant treated as in (*b*). Note foliaceous calyx and highly suppressed corolla. (× *c*. 2.)

PLATE 13

(*d*) *Cannabis sativa*. Flower from a male plant arising after treatment for a period of 48 hr. with CO at a concentration of 1 %. Central stamen with the connective prolonged into a stigmatic tip, the first indication of intersexuality. (× *c*. 15.)

(*e*) *C. sativa*. Highly intersexual flower from a genetically male plant treated as in (*d*). All stamens metamorphosed into carpelloid structures with long apical styles and small basal pollen sacs. (× *c*. 10.)

(*f*) *C. sativa*. Intersexual flower from a genetically male plant treated as in (*d*). Four stamens modified into carpelloid structures, one with a basal ovule (*A*); fifth stamen with fertile anther (*B*) and small apical stigmatic tips. (× *c*. 15.)

Problems of juvenility and flowering in trees. By P. F. WAREING.

Department of Botany, University College of Wales, Aberystwyth

In recent years there has been a marked awakening of interest in the problem of juvenility and flowering in trees, no doubt partly due to the focusing of attention on the subject by the need of tree-breeders to induce early flowering. The subject has recently been reviewed by Passecker (1947, 1954), Schaffalitzky de Muckadell (1954) and Robbins (1957). The following discussion does not purport to present an exhaustive review of the subject, but simply aims to enumerate and define the problems involved.

Our present knowledge of the physiology of flowering is largely derived from the study of photoperiodism and vernalization in herbaceous species. Such studies have given us some understanding of the role of external factors, such as daylength and temperature, in the transition from the vegetative to the flowering condition, though it must be admitted that even here our understanding is not very profound. In the so-called photoperiodically-sensitive species the transition to the flowering condition depends upon certain favourable daylength conditions, and in the absence of these conditions the daylength factor may become limiting, so that the plants remain permanently arrested in the vegetative state and are unable to go through their complete ontogenetic cycle. If such arrested plants are then given the necessary conditions the transition to flowering occurs and in this sense we can say that the change in daylength has 'caused' flowering. It is important to note that the conditions which favour vegetative growth are not necessarily those which are optimal for flowering and vice-versa. Thus, in vernalization the most favourable conditions for flower-induction may be too low for vegetative growth.

Not all species are equally sensitive to external conditions in their flowering behaviour, and in the so-called 'day-neutral' species flowering will occur over a very wide range of external conditions provided that the latter at least permit vegetative growth; conversely, it may be said that in such species flowering can only be prevented by conditions which are unfavourable to all growth. In a day-neutral species, such as sunflower, the seedling will form a certain number of leaves and then pass into the flowering condition, even if the external conditions are held *constant* throughout. That is to say, in such a species the change in the behaviour of the apical meristems is not occasioned by a change in external conditions, but must be brought about by some *endogenous* mechanism. It is evident that similar processes are also operative in those species which have certain specific daylength or temperature requirements for flower initiation, since it is known that the latter normally need to attain a certain stage of development before they will respond to external conditions—it is said that the plants need to attain a 'ripeness-to-flower' (Klebs, 1918) before they will flower in response to external conditions. Since the achievement of 'ripeness-to-flower' appears frequently to involve the attainment of a certain size or leaf-number, it is sometimes said that a 'size-factor' is involved. For example, Brussels sprouts cannot be vernalized until they have attained a certain minimum size (Stokes & Verkerk, 1951).

Although the final transition from the vegetative to the flowering condition is usually a fairly sharp one, nevertheless there are indications that the conditions within the plant are *gradually* moving towards the flowering conditions, as indicated, for example, by the gradient in such characters as leaf-shape (Allsopp, in press). We know nothing regarding the nature of the endogenous mechanism involved in such cases. Some have argued in favour of the view that it is a gradual change ('ageing') of the apex itself which is involved while others have favoured the view that it is the accumulation of *differentiated* tissue (e.g. leaf area) which is the primary factor. But even this most elementary problem remains unanswered.

When we turn to a consideration of the onset of flowering in woody species there appear to be certain resemblances with the situation in day-neutral herbaceous species. Thus, the seedlings of many if not all woody species exhibit a certain *juvenile* period during which they make active growth but remain vegetative. The transition to the flowering condition occurs only after a delay which varies greatly from species to species, ranging from 1 year in certain shrubs, to 30–40 years in forest trees such as beech (Table 1).

Table 1. *Duration of juvenile period in forest trees*

Species	Juvenile period (years)
Pinus sylvestris	5–10
Larix decidua	10–15
Pseudotsuga taxifolia	15–20
Picea abies	20–25
Abies alba	25–30
Betula pubescens	5–10
Fraxinus excelsior	15–20
Acer pseudoplatanus	15–20
Quercus robur	25–30
Fagus sylvatica	30–40

If one considers both trees and shrubs, there would appear to be a rough correlation between the duration of the juvenile period of a given species and its normal maximum size at maturity. Once a given tree commences flowering it normally continues to do so every year, although in certain species such as beech, flowering appears to be very sensitive to weather conditions and may occur irregularly. Thus, on the basis of the flowering behaviour we may distinguish between a *juvenile* and an *adult* (or mature) phase in the life history of the tree.

Differences between juvenile and adult stages are seen not only in flowering behaviour but also in various vegetative characters. Thus, it is well known that in certain species the leaf-shape of the juvenile phase is very different from that of the adult state, e.g. *Hedera*, *Morus*, *Acacia*, *Eucalyptus*, *Juniperus*, etc. In oak and beech there is a marked tendency for the dead leaves to be retained on the shoot of juvenile trees during the winter, whereas in the adult stages they are shed normally (Shaffalitzky de Muckadell, 1954). In some species the juvenile and adult conditions are distinguished by marked differences in phyllotaxis, e.g. *Hedera helix* L. Another morphological character which changes during ontogeny is the development of thorns, e.g. in *Citrus* the juvenile stages are commonly more thorny than the adult. Several anatomical differences between adult and juvenile stages have been reported; thus the leaves of seedling beech tend to be of the 'shade' type, irrespective of light conditions,whereas adult beech is capable of producing both types of leaf (Nordhausens, 1912; Schramm, 1912).

Among the physiological differences observed between juvenile and adult stages is the rooting ability of cuttings; it is very commonly found that whereas cuttings from young trees root readily, after a certain age this rooting ability is greatly diminished or entirely ost (Gardner, 1929).

An interesting feature of these phenomena is that the lower parts of the tree commonly retain the juvenile state after the upper parts have developed adult characters. This is, of course, well shown in ivy, where the lower regions of an erect-growing vine show the typical palmate type of leaf and are purely vegetative, whereas the upper parts show entire, ovate leaves and normally produce abundant flowering shoots. This differentiation into different regions showing diverse morphological and physiological characters was called *topophysis* by Molisch (1922). Attention has been drawn by various workers to the fact that the basal regions of the tree commonly remain permanently juvenile.

Not only is there apparent stability of the juvenile and adult states within the same plant body, but cuttings taken from the different regions and rooted continue to exhibit their juvenile or adult characters. This is well known to be true for ivy, for example. The same phenomenon is known to hold, for grafts, in those species which cannot readily be induced to form rooted cuttings. Thus, it has been shown by Schaffalitzky de Muckadell (1954) that juvenile scions of beech grafted on the top of tall trees continue to show their characteristic leaf-retaining habit. Conversely, it is found that scions from flowering regions of trees continue to flower when grafted on to quite small stocks. This is a common observation in forest-tree breeding and is known for species such as birch, larch, pine, etc. Likewise, it is known that scions from bearing fruit-trees grafted on to suitable root-stocks flower at an early age, whereas scions from young seedlings treated in the same way continue to remain vegetative. Although these facts are well known to tree-breeders, they have not received the attention they merit from those concerned with plant morphogenesis, for which the phenomena described have several important implications, which will be discussed below.

We have seen that the attainment of the adult condition by a seedling tree does not take place until the tree has attained a certain age, which is broadly characteristic for the species in question. Now this requirement for a certain age in the attainment of the adult condition might involve either (1) that the tree must go through a certain number of seasonal cycles of growth and dormancy and that the important factor in maturation is the number of *growth cycles*, or (2) the primary factor might be the attainment of a certain *size* and morphological complexity. By using modern techniques for growing plants under controlled environments, it is possible to obtain more than one annual growth cycle in a single calendar year by manipulating the daylength and temperature conditions. Doorenbos (1955) was able to reduce the juvenile period of *Rhododendron* by continuous growth under long days. Using controlled environment facilities, Bonner and Helmers[1] maintained seedlings of *Pinus taeda* L. in continuous growth under long-day conditions for a period of 2 years, when they had attained a large size, followed by a period of short-day treatment to induce dormancy. When the seedlings were again returned to long-day conditions they resumed growth and three female cones were produced. Another series of seedlings maintained under alternating shorter periods of growth and dormancy, so that they were exposed to several growth-cycles in a single calendar year, failed to flower.

A similar experiment was carried out by Longman and Wareing (unpublished) with seedlings of *Betula verrucosa* Ehrh. This species does not normally commence producing flowers until it is approximately 5–10 years old. Series of 3-month-old seedlings were grown under one of the following conditions:

(*a*) Grown continuously under18 hr. photoperiods in a greenhouse at 60–70° F.

(*b*) Grown in a greenhouse under long days until about 25 cm. in height, then exposed to short-days to induce dormancy. The plants were then chilled to break dormancy and the cycle repeated.

(*c*) Grown out of doors under natural daylength and temperature conditions.

One half of the plants of series (*a*) have remained in continuous growth from the time of germination in February 1957, whereas the remainder formed terminal resting buds in the winter of 1957/8 and had to be chilled before extension growth was resumed. At the end of March 1958, when the average height of these plants was about 3 m., four out of fourteen plants commenced to produce catkins and further catkins continued to be produced throughout the summer. Some of these catkins were borne on lateral shoots, but many were borne directly on the main axis. The first-formed catkins were male, but later ones were female and a few were bisexual. None of the plants of the 'periodic' series (*b*) or of the control series (*c*) have yet flowered, although the plants of series (*b*) have been exposed to 7 growth cycles, in a period of 27 calendar months. The results of this experiment would seem to indicate that the attainment of a certain absolute size is the primary factor determining the transition to the adult condition, and that it is not important whether this size is attained as a result of continuous growth or by the normal periodic succession of seasonal growth increments.

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[1] Report in *Nature, Lond.*, **180**, 892 (1957).

Before discussing further the possible role of size as a factor in the change from the juvenile to the adult condition, it is necessary to consider first certain other changes which occur during the ontogeny of the trees which are apparently of a different nature from the changes involved in the attainment of the adult condition. During the early years of growth of a seedling tree the annual growth increment is relatively large and increases logarithmically, but as the tree increases in size and complexity, the relative growth rate decreases and the annual growth increment begins to decrease. In the fully mature tree the annual growth increment is frequently very small indeed. This reduction in 'vigour' is also associated with a marked tendency to loss of apical dominance, in that there is no longer a clear differentiation between 'leaders' and laterals. Moreover, in the adult tree there is frequently much less tendency to the strong negative geotropism of young trees, so that the twigs are often orientated at random and may even hang downwards. Unlike such adult characters as leaf-shape and flowering-habit, however, these characteristics seen in the mature tree are, for the most part, *not* retained if a scion is taken from such a shoot-system and grafted on to a young stock. It is well known, for example, that if a scion is taken from a fruiting apple-tree, showing a complex spur-system with very little extension-growth, it undergoes a rapid 're-invigoration' when grafted on to a rootstock and shows a marked increase in annual growth increment; the resulting shoot-system usually shows a return of apical dominance, with well-marked leading shoots. Thus, the reduced vigour seen in the shoot-system of the fully developed tree is not a 'fixed' character in the sense that the leaf-shape and flowering-habit of the adult condition may be.

In order to make a clear distinction between the two types of phenomenon, it is proposed to refer to the transition from the juvenile to the adult state as '*maturation*', and the loss of vigour associated with the development of the tree as '*ageing*'. Thus, maturation involves a change to a relatively stable adult condition, whereas ageing involves effects which are easily reversed. We might say that maturation is analogous to 'genotypic' changes, whereas ageing corresponds rather to 'phenotypic' effects.

What is the cause of this universal phenomenon of ageing in trees? Now the curve for the whole tree throughout its life shows a typical sigmoid form. During its early years, the size of the tree tends to increase logarithmically, so that we get a well-marked 'exponential' phase of the growth curve. Later, however, the annual growth increment begins to decrease and the curve gradually 'flattens off'. One obvious explanation for the reduction in growth vigour with age, which is often advanced to account for the departure of the growth curve of a herbaceous species from the exponential phase, is that the proportion of 'non-productive' tissue, such as wood, gradually increases as the plant body increases in size (Heath, 1956). This effect is likely to be accentuated still further in a plant body which progressively increases in complexity over a period of many years. In the early stages, the number of shoot apices will tend to increase exponentially, and unless the supply of soil nutrients and overall synthetic ability of the plant increases correspondingly, severe competition between the various growth centres for both organic and inorganic nutrients will result. Evidence for such competition between the various growth centres of a shoot-system is seen in the fact that the 'thinning-out' of a branch shoot-system by pruning is well known from horticultural practice to result in increased growth of the remaining shoots. It has been postulated that a similar competition between growth centres occurs in herbaceous plants, such as cotton and barley, so that the level of nitrogen in the plant becomes limiting and results in a state of 'internal starvation' (Crowther, 1934).

If size is indeed the operative factor in the attainment of the adult condition, it is obviously important to know whether the minimum size for flowering is attained during the initial 'exponential' phase of the growth curve, or during the period when the relative growth rate is falling[1] and ageing is setting in, since the nutrient conditions in the tree are probably very different in these two stages of growth. If the onset of flowering occurs during the rising phase then it would seem that the absence of flowering during the early years may be due to the limiting levels of certain metabolites, which reach the necessary threshold levels as the synthetic capacity of the tree increases with its size. On the other hand, if the onset of reproduction occurs during the falling phase, or at least in shoots which show ageing, then it would seem more probable that flowering depends upon a *reduction* in the nutrient status of the tree. A consideration of the pattern of reproductive development in Scots Pine is significant in this connexion (Wareing, 1958).

In *Pinus sylvestris* the female cones first appear at the relatively early age of 5–10 years, and they are borne on strong leading shoots, sometimes on the main axis. Studies carried out by K. A. Longman and J. Moorby at Manchester indicate that there is a correlation between the appearance of female cones and the vigour of the tree. It seems clear, therefore, that the formation of female cones is associated with the 'rising phase' of the tree. But when we consider the development of the male condition we find a different situation. The male cones appear first in the basal region of lower branches (in the oldest part of the branch system) on shoots of a low morphological category. The more distal parts of these branches remain vegetative or bear female cones. As the age of the branch increases, however, male cones are found progressively higher on the branch, on laterals of increasingly higher morphological category, and may ultimately spread to the leading shoots, thus displacing the female cones. Since the male condition arises first in the older branches, a stage is frequently reached, in younger trees, in which the lower older branches are predominantly or entirely male and the upper branches female or vegetative.

Now when we compare the distribution of male cones with the data for ageing of the branches, we find that the first male cones appear in exactly those parts of the branch which show the most advanced ageing. Thus, if we study the annual growth increments in a 5-year-old branch of Scots Pine we find that the annual growth increment falls off rapidly in the laterals toward the base of the branch. This ageing effect is also reflected in the mean number of lateral shoots produced annually. In the lateral shoot-systems, the number of laterals per shoot falls rapidly in successive years, until ultimately the majority of shoots produce no laterals at all. The ageing process, as indicated both by the decrease in annual increment, and by the reduced production of laterals, is less rapid in the main axis of the branch, and is usually not yet apparent in a 5-year-old branch. The differential rate of ageing of the main branch axis of the laterals reflects the apical dominance of the axis and would seem to point to some correlative inhibition of the laterals by the main axis. Experiments at present being conducted by J. Moorby at Manchester suggest that this apical dominance may operate through the preferential transport of nutrients, including even mineral nutrients moving in the xylem, towards the leading shooting of the branch. Leyton & Armson (1955) have also shown that the leading shoots and young lateral shoots of Scots Pine have higher contents of N, P and K than the older laterals. There seems little doubt therefore, that the ageing of the tree results from a deterioration of the nutrient conditions in the branches, but the cause of this reduced nutrient status with age requires further elucidation.

The correlation between ageing and flowering in *P. sylvestris* strongly suggests that there may be a causal relationship between the two processes. It is not possible, in our present state of knowledge, to say how far the situation seen in *P. sylvestris* is applicable to other species, but there is no reason to believe that the cycle of development in this species is unique. It seems likely that in some species flowering depends on the attainment of a minimum size during the rising phase, as in the initiation of female cones in *P. sylvestris*. On the other hand, in other species it is likely that the attainment of the flowering condition depends upon a certain degree of ageing of the shoot-system. In those species in which flowering is dependent on ageing it is to be expected that the juvenile period will be longer than in those which initiate reproduction in the rising phase.

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[1] These two growth stages will be referred to as 'rising phase' and 'falling phase' respectively.

The importance of ageing in providing favourable conditions for flowering is seen not only in seedling trees but also in young grafted trees developed from scions from an adult tree. For example, with vigorous varieties of apple, flowering is frequently absent during the period of vigorous growth of young trees, and does not commence until vegetative vigour is reduced and a spur-system is developed. Thus it seems probable that ageing is important in providing favourable conditions for flowering even in trees which have already attained the adult condition.

An important question, which remains to be answered, is whether the ageing process, apart from providing conditions favourable to flowering, actually promotes the process of maturation. To put the question in a more general form, do various conditions which promote flowering, also hasten maturation? Certain horticultural evidence suggests that the answer may be in the affirmative. For example, several horticultural practices which check vegetative growth are known to hasten the onset of flowering in seedling trees. Such practices include grafting on to dwarfing rootstocks and bark-ringing (Kemmer, 1953). Such evidence is inconclusive, however, since it might be argued that in such instances where these practices were successful, the seedlings had already attained 'ripeness-to-flower' and that maturation was not the process which was hastened by these treatments.

The occurrence of relatively stable juvenile and adult states clearly raises problems of great biological interest. Although the phenomenon has been known for many years, especially in ivy, nevertheless sufficient attention has not been given to its implications for the general subject of morphogenesis. The phenomenon has tended to be regarded as an interesting, but relatively exceptional one, but closer consideration suggests that the occurrence of relatively stable alternative states in the tissue of single plant species is not uncommon. For example, in conifers such as *Larix*, *Picea*, *Pseudotsuga*, etc. the axis is normally vertically erect and shows radial symmetry in the distribution and orientation of both leaves and lateral shoots. The plagiotropic lateral shoots, on the other hand, show a dorsiventral arrangement of leaves and frequently also of the lateral shoots which they bear. Now when grafts or cuttings of erect and plagiotropic shoots are taken from the same tree, it is a common experience of forest tree breeders that these shoots continue to show the characteristic habit which they adopted on the parent, the plagiotropic shoots tending to bend over and grow more or less horizontally. The most famous example of this phenomenon exists at Munich Botanic Garden, where there is a plagiotropic branch of *Araucaria excelsa* R.Br. which was rooted by Goebel over 50 years ago and it still persists in growing plagiotropically. Thus, here again we have differentiation of the plant body into distinctive regions with contrasting morphological and growth characters and the retention of these characters even when the shoots are removed from the original plant body and grown independently. It seems probable that the basis of differentiation into erect and plagiotropic shoots is closely related to the processes determining differentiation into juvenile and adult regions, but the two phenomena are evidently not identical, since the appearance of plagiotropic shoots occurs at a very early age in seedling conifers, while they are undoubtedly still in the juvenile phase with respect to flowering. Again, the normal differentiation into root and shoot shows interesting parallels with the foregoing phenomena. Once the root and shoot apices have been established in the developing embryo they represent a very stable type of organization. Thus, it is very rare for a root apex to change into a shoot apex—regeneration of adventitious roots on shoots, or of adventitious buds on roots, occurs initially in parenchymatous tissue, and is not a change in an already organized apical meristem. The phenomenon of vernalization also shows certain similarities with juvenility in the sense that in many instances the change from the unvernalized to the vernalized condition is irreversible beyond a certain point in the development of the plant, and the vernalized condition is transmitted to all subsequently formed tissue. Certain of the phenomena of photoperiodic induction also seem to provide yet further examples of this sort.

All these phenomena seem to involve (1) the existence of tissues in two stable alternative states, (2) the transmission of a given state by cell-lineage through a large number of cell-generations.

Now although once the adult state has been attained in the shoot apex the state is transmitted by cell-lineage to all subsequently formed tissue, it is clear that the transition from the juvenile to the adult condition does not involve any *nuclear* genetic change, since the adult tissue ultimately produces embryos which are once again in the juvenile state. Hence we must conclude that the juvenile and adult conditions involve different states of the *cytoplasm* which are transmitted from one cell generation to another. It is not unreasonable, therefore, to postulate that self-duplicating cytoplasmic factors may be involved, such as have been postulated for various micro-organisms.

It might further be suggested that the transition from the juvenile to the adult conditions involves the disappearance of cytoplasmic particles which are concerned with certain metabolic processes, or alternatively the disappearance of certain adaptive enzymes. Although such speculations are at present difficult to test experimentally, nevertheless, it seems useful to have in mind models which would account for the observed facts.

Although it seems probable that it will be some years before we are able to determine the biochemical basis of juvenility, nevertheless certain recent observations may possibly provide a pointer to the solution of the problem. It has been seen that juvenile shoots of beech and oak tend to show failure of leaf abscission, and that with many species cuttings of juvenile shoots root more readily than adult. Now since it is known that auxins inhibit leaf abscission and promote rooting, these observations suggest that possibly juvenile shoots have a higher rate of auxin production. On the other hand, the recent demonstration by Brian (1959) that gibberellins inhibit leaf abscission suggests that possibly these growth substances are involved.

A further series of recent experiments also suggests that hormonal factors may be involved in juvenility. Doorenbos (1954) carried out experiments which involved grafting adult scions of ivy on to juvenile stocks and vice versa. He found rejuvenation of the adult scions and stocks, especially if leaves were left on the adult tissue, whereas the presence of leaves on the juvenile scions or stocks inhibited rejuvenation of the adult shoots. There was no apparent effect of the adult grafting partner on the juvenile parts. Frank & Renner (1956) found that when rooted cuttings of juvenile and adult shoots of ivy were put together in a vessel containing Knop's solution, the adult cuttings produced juvenile growth. This effect was only obtained when roots were present on the cuttings. Robbins (1957) has recently reported the reversion of adult shoots of ivy to the juvenile condition following treatment with gibberellic acid. These various results open up a number of possible new lines of approach to the problem.

There are many signs of renewed interest in the problem of juvenility in woody plants, and it seems likely that in the future we shall see rapid advances in our knowledge of a phenomenon which is of great importance both to the tree-breeder and to the student of developmental physiology and morphogenesis.

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Temperature-induced meristic and other variation in Cannabis sativa.

By Y. Heslop-Harrison and I. Woods
Department of Botany, Queen's University, Belfast

(With 2 Text-figures)

Introduction

During an investigation of the effects of environmental factors upon sex expression in the dioecious *Cannabis sativa* L. (hemp), it has been found that morphogenetic anomalies, not necessarily connected with sexuality, arise in the flowers of genetically male plants in certain combinations of photoperiod and temperature. The phenomenon is most apparent when photoperiods provoking rapid flowering are combined with low night temperature. Under these conditions, a high proportion of the flowers formed is intersexual, but in addition, even amongst those which are structurally mainly male, the majority shows meristic anomalies and various forms of fusion and adnation. The morphology of the induced intersexes will be treated elsewhere; the present paper concerns the induced variation in flower architecture not directly connected with the character of the floral appendages.

Materials and methods

The hemp strain used in these experiments is of Portuguese origin, apparently originally selected for fibre production. It has been inbred at Belfast for eight generations, with rigid selection for uniform photoperiodic response and freedom from morphological anomaly.

Seeds were germinated in vermiculite, and the seedlings transferred at an age of 5–6 days to a peat-sand mixture in individual plastic containers, where they received a standard ration of a balanced nutrient solution every third day.

The plants were grown throughout in controlled-environment chambers. Light was supplied during the 'day' periods from batteries of warm-white fluorescent tubes, the level of the plants being adjusted at intervals to maintain an intensity of 1000–1100 f.c. at the apices. Air temperature during the day was regulated at 22° C., and the relative humidity was maintained at 75 %. Plants receiving 'warm' nights experienced the same air temperature and relative humidity during the dark period. Those receiving 'cool' nights were transferred at the onset of the dark period to chambers with air temperature regulated at 10° C. The relative humidity in these cool chambers normally dropped from 75 % at 5 p.m. to *c.* 50 % at 9 a.m.

For the first 20 days after transplanting to individual containers, all plants were grown in an air temperature of 22° C. with two daily light periods of 8 hr. spaced by 4 hr. dark periods. Under these 'long-day' conditions they remained strictly vegetative, and had uniformly opened leaves to the third node by the end of the 20-day period. Subsequently, flowering was induced by eliminating one of the daily light periods, and during the period of induction one group experienced night temperatures of 10° C., while another remained throughout at 22° C.

Observations

The male plants of the 'warm'-night series flowered actively from the twelfth day of induction, whilst those receiving 'cool' nights were delayed 12–14 days. Samples of flowers were removed at intervals during the flowering period until a minimum of 25 had been accumulated for each plant. Each flower was examined in the fresh state for anomalies in perianth and androecium, both in numbers of members and their cohesion or imperfect separation.

Meristic anomalies. Mean tepal and stamen numbers for the pooled samples from six male plants from each of the two series are compared in Table 1, and also the within-plant variances. Both in perianth and androecium the mean number is slightly but significantly lower in the plants receiving cool nights, but the impressive differences are in the variances—substantially greater for both perianth and androecium in the plants under cool nights.

Table 1. *Means and within-plant variances for tepals and stamens of male plants of hemp under photoperiods of 8 hr., day temperature 22° C., and night temperatures of 22 and* 10° C.

(Six plants per series, samples of 25–70 flowers per plant.)

Night temperature (° C.)	Perianth		Androecium		Degrees of freedom
	Mean tepal no.	Within-plant variance	Mean stamen no.	Within-plant variance	
22	4·98 ± 0·008	0·0185	4·96 ± 0·012	0·0437	263
10	4·78 ± 0·037	0·3289	4·67 ± 0·055	0·6601	245

Differences in means and variances between the two series significant at the 5 % level for both perianth and androecium.

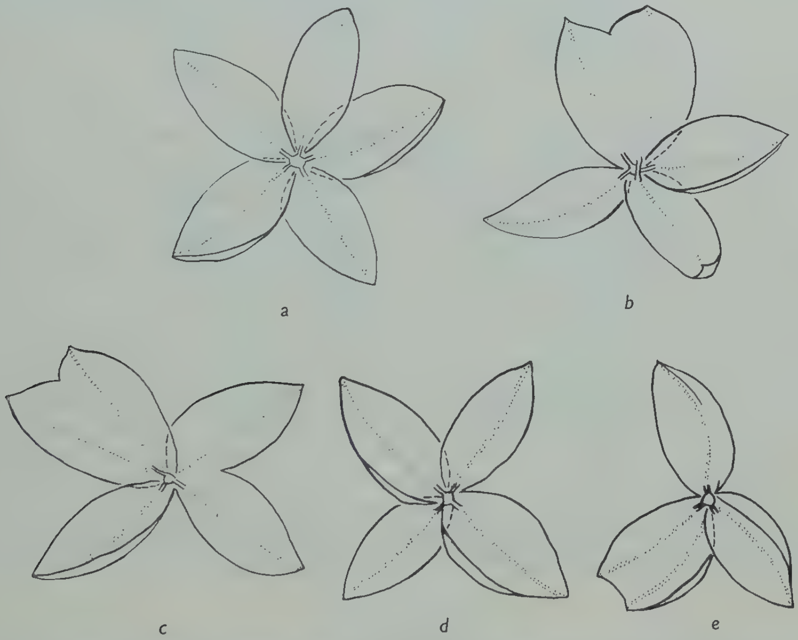

Fig. 1. (*a*) Perianth from normal male flower. (*b*–*e*) Perianths from flowers of male plants exposed to low night temperatures during photoperiodic induction. (× c. 5.)

Branching and cohesion of floral members. Of a total of 251 flowers from the male plants receiving cool nights during induction to flower, 37·1 % showed incomplete separation of the tepals (Fig. 1), and 22·4 % incomplete separation of the stamens (Fig. 2). No general distinction can be made between 'branching' and 'cohesion' in the androecia of these anomalous flowers, since all situations appear between that in which two or more otherwise normal stamens have united filaments (Fig. 2*e*, *f*) and that where there is merely some degree of apical forking (Fig. 2*b*).

Correlations. The incidence of anomalies in perianth and androecium proved not to be independent in the flowers of male plants experiencing cool nights. Over the range four to six members, meristic variation in perianth and in androecium were strongly associated with a $\chi^2 = 187{\cdot}38, P < 0{\cdot}01$. The association between the occurrence of cohesion of parts in perianth and in androecium was less strong but still significant, with a $\chi^2 = 17{\cdot}46, P < 0{\cdot}01$.

Surprisingly, meristic variation and the incidence of cohesion of parts were not associated in either perianth or androecium. For the perianth, $\chi^2 = 0{\cdot}1041, P > 0{\cdot}01$, and for the androecium, $\chi^2 = 0{\cdot}0003, P > 0{\cdot}01$.

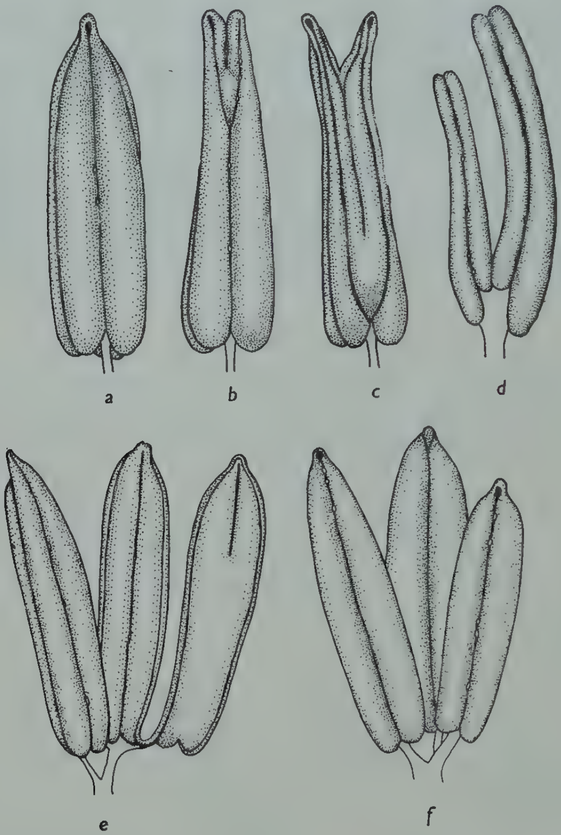

Fig. 2. (*a*) Normal stamen. (*b–f*) Stamens from flowers of male plants exposed to low night temperatures during photoperiodic induction, showing various forms of branching and fusion. (× *c*. 12.)

Discussion

As already mentioned, one of the principal effects of low night temperatures experienced during or immediately after photoperiodic induction in male plants of hemp is to induce intersexuality in a high proportion of flowers. Intersexuality in male flowers involves a transformation of stamens to carpellate or intermediate structures; the phenomena described here concern not the character of the floral members, but their numbers and cohesion.

The comparison of the within-plant variances shows that the effect, so far as it concerns numbers of parts, is upon the developmental regulation of individual plants. In some manner, not directly illuminated by these experiments, the systems of growth fields which establish pentamery in flower primordia are upset, so that in one and the same inflorescence flowers varying widely in numbers of components arise. A form of explanation can be given in general terms by supposing that the meristic properties of flowers are determined by the establishment of growth fields in the primordia, and that should the period during which this is proceeding coincide with a sudden variation in some key environmental factor, such as temperature, a modification may be introduced in the temporarily labile system which will subsequently register a permanent effect in the type of flower formed. It is noteworthy that the air temperature changes were abrupt during this experiment; the smooth diurnal cycle of temperature variation which a plant might experience in nature cannot readily be simulated in growth chambers.

So far as the whole plant is concerned, the effect of low night temperature is to increase the variance in tepal and stamen numbers very considerably whilst producing only a small shift in the means; evidently there is no question of the system of flower morphogenesis being deflected in some particular direction, say by a differential effect upon the rate of two interacting processes. It seems rather that a new source of variance is introduced, affecting the character of individual flowers according to the time their primordia pass through the critical phase in relation to the diurnal temperature cycle. It seems important to make this distinction, for the other effects of low night temperatures, the provocation of intersexuality in the flowers of male plants, does mark a shift of the ontogenetic path of certain flower primordia in a particular direction; it does not represent merely an amplification of general variability.

As an example of a break-down of developmental regulation under environmental stress in an inbred line of a normally outbreeding species, these results with hemp are of some interest genetically. It has recently come to be rather widely accepted that heterozygosity, *per se*, may play some role in maintaining a high level of developmental homeostasis (Thoday, 1953; Lerner, 1954), although Waddington (1957) points out that 'homeorhesis', as a general principle of epigenetics, must have a considerably wider basis than simply dependence on heterozygosity. The evidence that some importance does attach to heterozygosity in this context comes from experiments such as those of Mather (1950, 1955) in which the incidence of intra-individual variation in style length in *Primula* and body symmetry in *Drosophila* has been shown to be more pronounced in inbreds than crossbreds. No attempt has yet been made to compare the reactions of the present inbred hemp strain with those of an outbred population in these special conditions of photo- and thermoperiod, but clearly it would be informative to do so, not only to establish whether the latter showed better developmental regulation in respect to meristic properties, but to discover whether its resistance to sex change under these conditions would be greater. It may be significant that the male is heterogametic in hemp, and that the floral organization, both in numbers and character of appendages, is always more readily influenced in male than in female individuals, which show a remarkable stability in flower morphogenesis under a wide range of conditions.

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Factors controlling the growth and form of fruits. By L. C. Luckwill

Long Ashton Research Station, University of Bristol

(With 4 Text-figures)

Introduction

The scientific exploration of a morphological problem, as indeed of any problem in biology, normally proceeds in three stages: first, the observation of the facts; secondly, the formulation of a working hypothesis which might explain and correlate the facts; and thirdly, the carrying out of experiments to test the hypothesis; and it is in this sequence that I propose to deal with the problem of growth and form in fruits.

Because many are of economic importance, fruits have probably been studied more intensively than most other organs of the plant. A great deal of information exists on the way in which fruits grow, on their chemical constitution, their gas exchange, and on the metabolic changes accompanying growth and ripening, but our knowledge of the hormonal factors which control these processes is still very fragmentary and presents a fascinating challenge to the experimental morphologist.

The fruit, unlike other organs of the plant, is not a clearly defined morphological unit, and for the purposes of this paper I shall follow Nitsch (1952) in describing it simply as 'the structural entity resulting from the (post-floral) development of the tissues which support the ovules'.

Increase in size

The most obvious thing about the growth of a fruit is that it involves very large increases in volume. This is particularly true of cultivated fruits such as the black currant which, in a period of 10 weeks undergoes a 100-fold increase, or the apple which may increase its volume 6000 times during a growing period of only twenty weeks. By plotting the volume or weight of the fruit against time we obtain a growth curve which falls into one of two distinct types. In some plants, e.g. cucumber, tomato, apple (Fig. 3), the growth of the fruit during the post-fertilization period can be represented by a smooth sigmoid curve, such as characterizes the growth of many plant organs. In others, e.g. *Prunus* spp., the fig (Fig. 4), blueberry, fruit growth proceeds in three distinct phases, two periods of rapid growth being separated by an intermediate period of varying length when little or no increase in volume occurs. The growth curves of such fruits may be interpreted as made up of two successive sigmoid-type curves.

The increases in volume associated with the growth of fruits are due partly to increases in the number of cells and partly to increase in cell size, though in some fruits (e.g. apple) expansion of the intercellular spaces may also contribute to the growth of the fruit during the later stages. In general, growth by cell division predominates in the early stages and growth by cell expansion in the later stages, though there are many variations on this general theme. In *Lycopersicon esculentum* Mill. cell multiplication ceases at anthesis, the whole of the post-floral development being attributable to cell expansion, whereas in the closely related *L. pimpinellifolium* Mill. some cell division continues right up to maturity (Houghtaling, 1935). In the apple, cell division ceases 3–4 weeks after bloom (Bain & Robertson, 1950), and in *Cucurbita moschata* Duch. when the fruit reaches 9 cm. in diameter (Kano, Fujimura, Hirose & Tsukamoto 1957). The change from cell division to cell extension growth may thus occur at different times in the development of different fruits. The change, when it does occur, is frequently quite abrupt, as is shown by the work of Kano *et al.* (1957), who have applied the differential growth formula of Huxley (1932) to the study of the relationship between cell size and fruit size in certain members of the Solanaceae and Cucurbitaceae (Fig. 1). In some fruits more complicated patterns of development are found in which cell division may cease at different times in different parts of the fruit. Thus, in the strawberry, cell division in the cortex ceases just before anthesis, whereas in the pith it continues right up to maturity (Havis, 1943). In the Deglet Noor date general cell division throughout the mesocarp terminates 6 weeks after flowering, but a localized region of meristematic activity at the base of the fruit persists for a further 6 weeks (Long, 1943).

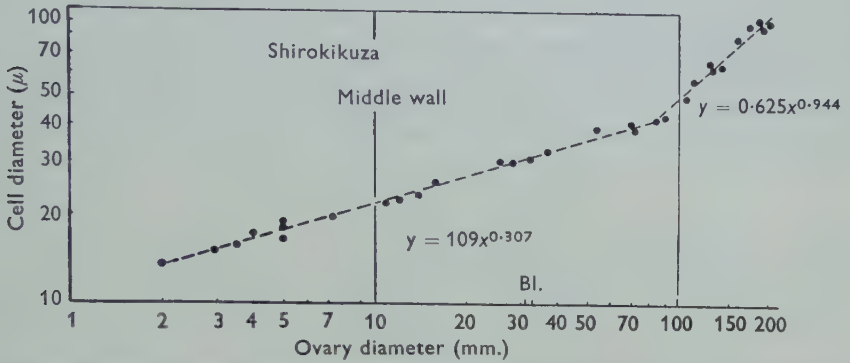

Fig. 1. The relation of cell diameter to fruit diameter in the middle wall of the Shirokikuza cushaw (*Curcubita moschata* Duch.). From Kano *et al.* (1957).

SHAPE DETERMINATION

Broadly speaking, two main types of shape determination are found in fruits. In the simplest type, exemplified by the cucumber and tomato, the shape at maturity is already pre-determined in the ovary at the time of flowering. This means that during its post-floral development the fruit grows at an equal rate in all directions. More commonly shape differences arise after flowering as the result of unequal growth rates in different dimensions, so that the shape index, or length/breadth ratio, is changing continuously during growth, as in the egg plant (Kano *et al.* 1957) and *Capsicum* (Kaiser, 1935), the elongated fruits of which arise from ovaries which are approximately spherical in shape.

Although the size and shape of fruit typical of a particular species is determined genetically, both these characters are liable to modification within rather wide limits within the genotype by diverse external and internal factors. Of the external factors modifying size, nutrition is of obvious importance, and in some fruits (e.g. apple) shape may be modified by unilateral light or gravitational forces (Schander, 1955*a*). Of the internal factors, by far the most important is the number and distribution of seeds within the fruit.

INFLUENCE OF SEEDS ON FRUIT GROWTH

The dependence of fruit size on seed number is a rather general phenomenon though the relationship may be masked in some fruits (e.g. certain varieties of *Citrus*) in which there is an inherent tendency to parthenocarpy. The correlation is very marked in grapes (Müller-Thurgau, 1898) and other few-seeded fruits, though, even in the many-seeded black currant, correlation coefficients ranging from 0·86 to 0·98 were found between seed number and the diameter of the mature berry (Teaotia & Luckwill, 1956). In apples the relation between fruit size and seed number is more complex: in some varieties the relationship is masked by parthenocarpic tendencies, whilst in others, negative as well as positive correlations have been reported. Usually, where the seed content is low, a stimulating effect of seeds on flesh development can be demonstrated, but high seed numbers may depress fruit growth through competition for available carbohydrates (Schander, 1956).

The influence of seeds on the shape of fruits is particularly well shown in certain pears in which, for genetical reasons, many of the seeds may abort before reaching maturity. Schander (1955 *c*) has found that the earlier in their development the seeds abort, the more elongated is the fruit in relation to its breadth (Fig. 2). Occasionally, as a result of frost at blossom time, the seeds are killed at a very early stage of growth and the fruits which subsequently develop are sausage-shaped rather than pyriform. The influence of seeds on the growth of the flesh is often strictly local in its effect, so that an uneven distribution of seeds may result in asymmetrical growth of the fruit. In *Prunus* spp. for instance, failure of one of the two ovules to develop results in unequal growth of the carpel wall on opposite sides (Tukey, 1936), and in the apple asymmetry is attributable principally to the failure of seed development in one or more of the five carpels. The local effect of the seeds is very clearly seen in strawberries in which, owing to insufficient pollination, only a small number of fertile achenes have developed. In such fruits the receptacle tissue expands only in the immediate vicinity of these fertile achenes, giving rise to extremely distorted fruits. Many other instances could be quoted of the influence of seeds, not only on the size and shape of fruits, but also on the chemical composition of the flesh and the time of ripening.

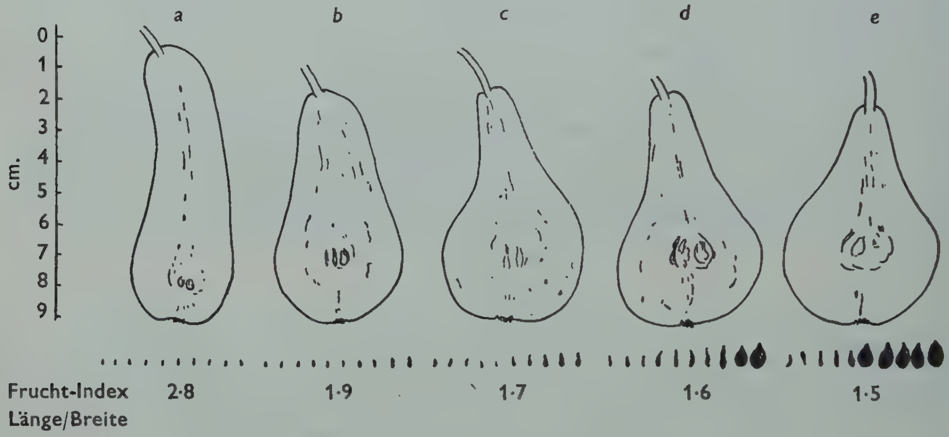

Fig. 2. The relationship between seed abortion and fruit shape in Conference pear. From Schander (1955 *c*).

Auxins and fruit growth

The work which I have so far described constitutes the observational phase of our problem. Having surveyed the main facts of fruit growth we are now ready to proceed to the second phase—the formulation of an hypothesis which might explain and coordinate these facts. We have seen that fruits grow largely by a process of cell expansion supplemented by cell division in the early stages, and that the direction and amount of growth are strongly influenced by the seeds. This suggests that the seeds are the source of a hormone-like substance capable of stimulating the growth of the adjacent tissues of the fruit. The principal hormones known to control cell extension in plants are the auxins. Auxins also influence cell division, for example in the cambium of woody stems and in the initiation of adventitious root primordia. In the stem and the root they have their origin in the terminal meristems. In the fruit we have no terminal meristem, but we do have two very active internal meristems, the growing embryo and the endosperm, both of which grow by cell division. A reasonable hypothesis therefore would seem to be that these meristematic centres in the growing seeds produce auxins and that these auxins. pass out of the seeds either along the vascular system or by diffusion through the testa, and directly stimulate the growth of the surrounding tissues of the fruit.

We may note in passing that there exists a considerable body of indirect experimental evidence in support of the idea that auxins are limiting factors in fruit growth. Thus, in some fruits, though not in all, fruit development in the absence of fertilization may be stimulated by the application of various synthetic auxins. The application of auxin sprays to partially grown fruits at certain stages of development may in some species result in an increase in the growth rate and in the final size attained, a technique which has found commercial application for certain varieties of oranges, apricots, figs and grapes. In other fruits, such as blackberry and strawberry, auxin applications have proved of value in increasing fruit size where, owing to partial sterility or inadequate pollination, the seed content and growth rate of the fruit is below normal.

Evidence of this type, based on the effects of synthetic auxins, most of which differ chemically from their endogenous counterparts, whilst not providing proof of the auxin hypothesis of fruit growth outlined above, does at least make it appear that the hypothesis is a reasonable one. More direct evidence comes from the results of experiments in which measurements have been made of auxin production in the seeds, and especially from those in which such measurements have been accompanied by simultaneous observations on fruit growth. One of the earliest workers in this field was Gustafson (1939) who showed that in immature fruits of the tomato the concentration of auxin in the seeds was very much higher than in the placenta, and that the concentration in the placenta, central axis and partitions of the fruit, was in turn higher than that in the carpel wall. Such centrifugal gradients of auxin concentration within the fruit are consistent with the idea that auxin is being synthesized in the seeds and is moving outwards along a concentration gradient to the other parts of the fruit.

Table 1. *Auxin distribution in immature tomato fruits in μg. equivalents IAA per kg. fresh wt.*

(Gustafson, 1939)

	Fruit 1	Fruit 2
Seeds	15·33	30·03
Locular jelly	6·57	0·45
Placentae	2·44	2·47
Central axis and partitions	2·27	2·69
Carpel wall	1·27	0·63

In my own experiments with apples (Luckwill, 1948, 1953) measurements of auxin concentration in the seed were made at weekly intervals throughout the growing season and simultaneous measurements were made of embryo and endosperm development, fruit growth and the rate of fruit abscission. The results of these experiments, made over a period of 4 years on a number of different apple varieties, may be summarized as follows:

(1) The auxin content of the seeds during the first 3–4 weeks after fertilization is very low. It then rises to a sharp peak and falls again, rising to a second peak 3–5 weeks later (Fig. 3).

(2) The amount of auxin found in the seed at any given time is approximately proportional to the amount of cellular endosperm tissue present. The auxin concentration in the endosperm is considerably higher than in the embryo (Table 2).

(3) The sharp fluctuations in seed auxin are not reflected in any corresponding changes in the fruit itself, the growth of which may be represented by a smooth sigmoid curve (Fig. 3).

(4) The changes in auxin level in the seeds are negatively correlated with the rate of fruit drop, in so far as the periods of maximal auxin production invariably correspond with the periods of minimal fruit drop.

More recent studies of the same type with the fruit of the Calimyrna fig (Crane, Bradley & Luckwill 1959) have led to essentially the same conclusions. Here again very low auxin concentrations were found during the early stages of fruit growth, followed by a sharp increase at the time of endosperm formation, after which the auxin level again fell (Fig. 4). As in the apple, no correlation appeared to exist between the growth rate of the fruit and the auxin concentration, and no evidence was found that lack of auxin was a limiting factor during the second stage of development of the fruit, when little or no increase in size occurs.

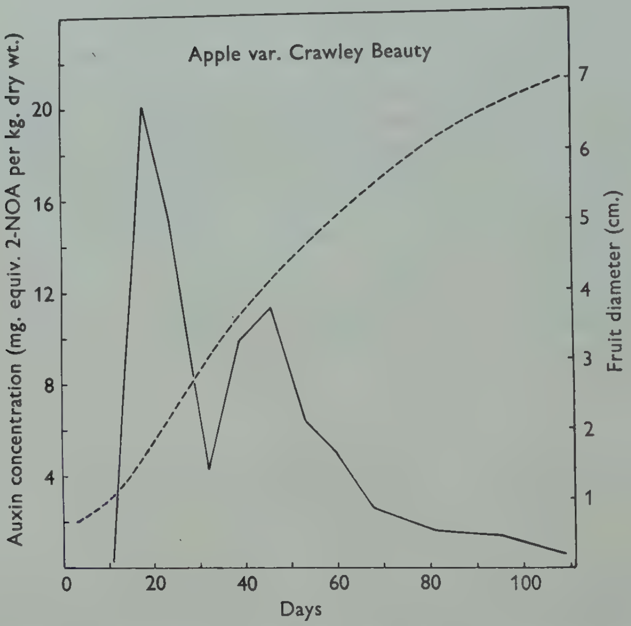

Fig. 3. Changes in auxin concentration in the seeds (full line) and fruit diameter (broken line) in apple var. Crawley Beauty, in relation to days after petal-fall. From Luckwill (1953).

Table 2. *Auxin content of the embryo and endosperm in partially developed seeds of the apple, as μg. equivalents 2-NOA*

(Luckwill, 1948)

Variety and date	Part of seed	Total auxin Per 100 seeds	Total auxin Per g. dry wt.
Miller's Seedling,	Embryo	15·2	15·2
7 August	Endosperm	55·4	277·0
Crawley Beauty,	Embryo	0·8	0·9
12 August	Endosperm	2·4	7·1

A very similar situation exists in the strawberry (Nitsch, 1950, 1952) where a very sharp rise in the auxin content of the achenes at the time of endosperm formation appears to be quite unrelated to the general growth pattern of the fruit (Fig. 4).

The results of experiments with these three diverse types of fruit, therefore, are in agreement with the concept of the seed as a centre of auxin production in the fruit. They also suggest that the endosperm is by far the most important, and perhaps the only, auxin producing tissue within the seed. On the other hand, they clearly do not support the second part of our hypothesis that auxin is the chief factor concerned in the control of fruit growth, though in the deciduous apple there is good evidence that it does control fruit abscission. What interpretation should we put upon these results?

First, it is important to realize that the 'auxin' we extract from plant tissue by water or organic solvents is not a simple chemical substance but a rather complex mixture of several different compounds having auxin-like properties, which can be separated by chromatographic techniques. Indole-3-acetic acid (IAA), at one time thought to be the dominant, and perhaps the only naturally occurring auxin, is now known to be only one of a number of hormones with similar biological properties which occur in plant extracts. In some species even IAA appears to be absent (Luckwill & Powell, 1956). Secondly, not all the auxins which we extract from plants necessarily function as such in the species which produce them. A good example of this is indoleacetonitrile which may be extracted in relatively large amounts from cabbage and detected by its ability to induce the elongation of oat coleoptiles, but which is nevertheless inactive when tested on the tissue of the cabbage itself. The reason for this apparent anomaly is that the activity of indoleacetonitrile depends on its enzymatic conversion to IAA, and that only certain tissues are able to effect this conversion. In fruits, therefore, it is possible that some of the endogenous auxins we extract from seeds are inactive on fruit tissue, and that fruit growth may be correlated with only certain components of the auxin complex, rather than with total auxin. This is suggested by the work of Wright (1956) on the development of the black currant berry, in which three principal auxins occur. Of these three auxins, two show a possible relationship with the growth curve of the fruit whilst the third, which at some stages of development accounts for the greater part of the total auxin, is quite unrelated. A similar chromatographic analysis of the auxins of the fig, on the other hand,

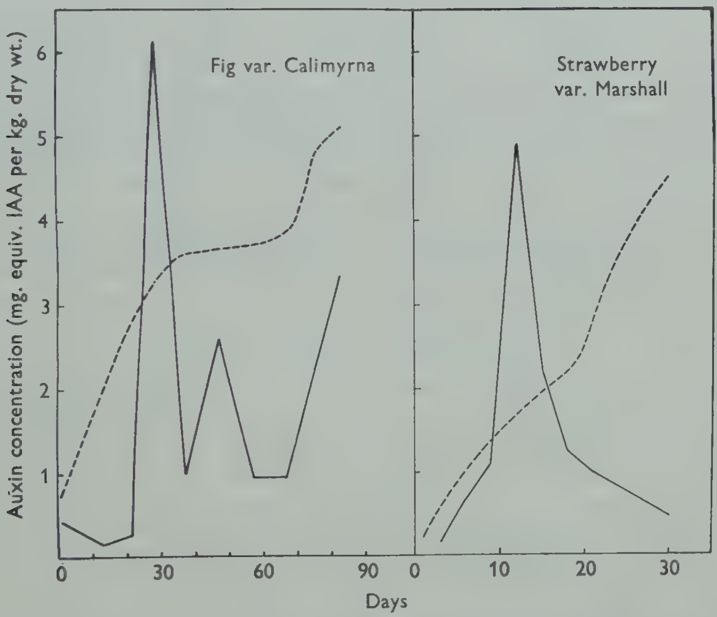

Fig. 4. Changes in auxin concentration (full line) and fruit diameter (broken line) in the Calimyrna fig (Crane, Bradley & Luckwill, 1959), and the Marshall strawberry (Nitsch, 1950).

failed to reveal a relationship between any particular auxin and the growth of the fruit: there was, in fact, no essential quantitative or qualitative difference between the auxin pattern during stage 2, when growth is minimal, and that during stage 3 when very active expansion is taking place (Crane *et al.* 1959).

This then is the present position: in spite of the large body of supporting evidence, derived mostly from experiments with synthetic auxins, studies of endogenous auxins in fruits and seeds do not suggest that, in general, these substances are normally limiting factors in the growth of fruits, though they are undoubtedly active in controlling fruit abscission. Particularly difficult to explain on the 'auxin hypothesis' is the essentially similar auxin pattern found in fruits such as the apple and the fig, the growth curves of which are quite dissimilar. It now appears that we may have to modify our original hypothesis and to inquire whether there are other types of growth factors besides auxins which occur in seeds and which might be active, either alone or in combination with auxin, in stimulating fruit growth.

Other growth factors

Besides auxins two other types of growth factors are now known to occur in the seeds of at least certain species of plants. The liquid endosperm of the coconut contains a complex of factors which are active in stimulating cell division in certain types of tissue culture (Steward & Caplin, 1954) and which exhibit marked synergism with synthetic auxins (Shantz, Steward, Smith & Wain, 1955). These coconut milk factors appear to be essential for the *in vitro* culture of immature plant embryos and it seems likely that their natural function in the plant may also be concerned with embryo development. Although they have been shown to occur in the free nuclear endosperms of a number of species besides the coconut (Steward & Caplin, 1954) it has not yet been demonstrated that they have any activity in stimulating the growth of fruit tissue. Recent attempts to induce parthenocarpic development of fruits such as apples and pears by means of coconut milk extracts, alone and in combination with synthetic auxins, have proved unsuccessful.

The gibberellins, on the other hand, are undoubtedly active in stimulating fruit growth. Gibberellin A_3 (gibberellic acid) is effective in stimulating parthenocarpy in tomato (Wittwer & Bukovac, 1958) and, under certain conditions, it shows synergism with IAA: it will stimulate parthenocarpy in the fig (Crane, 1958) and increase the growth rate and final size of certain seedless varieties of *vinifera* grapes (Weaver, 1958): it has also been reported as active in increasing fruit-set in pears (Wittwer & Bukovac, 1958) and in several citrus fruits (Hield, Goggins & Garber, 1958; Soost, 1958). After many unsuccessful attempts to stimulate parthenocarpy in apples with auxins I have recently had some success with gibberellic acid. In these experiments, which were of an exploratory nature only, pollination was prevented by cutting off the styles before the flowers opened. A few days later the whole tree received a spray application of 100 parts/million GA. The parthenocarpic fruits that developed were noticeably more elongated than the pollinated controls, though they developed at the same rate and matured at about the same time.

Not only are gibberellins active in stimulating fruit growth, but evidence is accumulating for the rather widespread occurrence of substances with gibberellin-like properties in seeds. So far, such substances have been found in the seeds of *Echinocystis*, (West & Phinney 1956), *Phaseolus* (Radley, 1958), peas (Radley, 1958), wheat (Radley 1958), and coconut (Radley & Dear, 1958), though in none of these plants has the occurrence of the growth factor been studied in relation to seed and fruit development. Until this has been done any speculations as to the possible role of naturally occurring gibberellins in the control of fruit growth must, of necessity, be tentative. However, in conclusion, I think we can say that these recent investigations of this new type of growth-regulating compound have opened up an entirely new and promising experimental approach to this fascinating and economically important problem of the control of growth and form in fruits.

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On the genera of the Ulvales and the status of the order[1]

By GEORGE F. PAPENFUSS

Department of Botany, University of California, Berkeley, California

Communicated by the Botanical Secretary

The order Ulvales Blackman & Tansley (1902) is usually considered to comprise the genera *Ulva* Linnaeus (1753), *Letterstedtia* J. E. Areschoug (1851*a*), *Monostroma* Thuret (1854), *Enteromorpha* Link (1820), *Percursaria* Bory (1823, 1828) and *Capsosiphon* Gobi (1879). In recent times the following genera have been added to the order: *Blidingia* Kylin (1947), *Rhizenteron* Dangeard (1952*a*, *b*), *Lobata* Chapman (1952), *Gemina* Chapman (1952) and *Feldmannodora* Chadefaud (1957).

ULVA

It is hardly believable that so much should be wrong with the nomenclature of such a classical and ubiquitous genus as *Ulva*. *Ulva* is one of the four oldest of the genera of algae. Along with *Fucus*, *Conferva* and *Chara*, it dates from the starting-point of botanical nomenclature, namely, the first edition of Linnaeus's *Species Plantarum*.

Linnaeus assigned nine species to *Ulva*. In the course of time, six of them were removed to other genera (cf. Silva, 1952, p. 294). Of the remaining three species (*U. linza*, *U. latissima* and *U. lactuca*) one, *U. linza*, is regarded as a species of *Ulva* by some authors and as a species of *Enteromorpha* by others. *Ulva latissima* is regarded by most authors as a variety of *U. lactuca*. I have seen the type of *U. latissima* in the Linnaean Herbarium (no. 1275–14 of Savage's (1945) catalogue of the Linnaean Herbarium), and can confirm the observation of Turner (1811, p. 72) and the inference of Silva (1952, p. 296) that the specimen is representative of *Laminaria saccharina* (L.) Lamouroux.

Through the process of removal, *Ulva lactuca* thus remained the only Linnaean species seemingly representative of *Ulva* as currently circumscribed and it has consequently served as the type of the genus.

Such typification, however, is entirely contrary to Linnaeus's diagnosis of *Ulva*. In the *Genera Plantarum* (1754, p. 492), where the genus was characterized for the first time, Linnaeus stated that the fructifications were in a vesicular membrane, which shows that he regarded the genus as typically composed of plants that are hollow.

In his excellent introduction to the recently published facsimile edition of Linnaeus's *Species Plantarum*, Stearn (1957) devotes a chapter to the *Genera Plantarum* and the typification of Linnaean genera. He points out (p. 37) that the descriptions of genera by Linnaeus '...rarely cover a whole generic concept...many genera, even the largest, have descriptions that have clearly been drawn from single species...'. In conformity with the Code, it is essential that a species be chosen which fits the generic diagnosis.

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Hence *Ulva* should be typified by one of the hollow species and not with *U. latissim* as C. Agardh (1822, p. 402) proposed. The first species listed by Linnaeus in the *Specie Plantarum* was *U. intestinalis*. It seems highly probable that Linnaeus drew his diagnos of *Ulva* especially from this species and that it should serve as lectotype of *Ulva*. O this basis *Ulva* becomes a synonym of the conserved name *Enteromorpha* Link (1820) which also has *U. intestinalis* as lectotype (cf. Silva, 1952, p. 294).

To retain the current concept of *Ulva* (namely, a genus comprising plants that ar distromatic with the two cell-layers adhering to each other) it is necessary therefore tha the name be conserved as of a later author and that *Ulva* Linnaeus be included in the rejected names against *Enteromorpha* Link. I propose that the name *Ulva* be conserved in the sense of Thuret, who in 1854 revised *Ulva* by removing from it the monostromatic species for which he established the genus *Monostroma*.

The next question concerns the identity of *Ulva lactuca*. During the past two centuries there has been a good deal of disagreement among workers as to which taxon Linnaeus had in hand when he described *U. lactuca*. No one appears to have searched for or studied the type. From what is known of Linnaeus's method of work (cf. Stearn, 1957, p. 126) it is quite clear that he had a specimen in front of him when he drew up the diagnosis. The species should thus be typified if possible with a specimen in his herbarium, if one is present, and not with one in the herbarium of one of the authors cited by him. Since neither Jackson (1912) nor Savage (1945) lists a Linnaean specimen of *U. lactuca*, it seemed likely that the type might be lacking in the Linnaean Herbarium. However, in 1954 I found the type in the Linnaean Herbarium. It is the specimen marked '5' in Linnaeus's hand (no. 1275–24 of Savage's catalogue). This specimen agrees well with Linnaeus's description of the species, and furthermore '5' is the number assigned to *U. lactuca* by Linnaeus in the *Species Plantarum*.

At my request Dr C. R. Metcalfe, the Botanical Secretary of the Linnean Society, kindly agreed to have sections made of this specimen. These sections showed a distromatic condition (Text-figs. 1, 2) with hyaline rhizoids sparsely present between the two layers of cells in some areas (Text-fig. 1). The presence of occasional rhizoids between the cell-layers was puzzling at first since such structures are not known to occur in conventional *Ulva* but are a feature of *Letterstedtia*, which genus, however, I consider the same as *Ulva*. As is well known, the cells of the thallus of *Ulva* immediately above the holdfast send out from the inner face descending rhizoids which form a thick medulla at the base of the frond and farther down constitute the holdfast. Examination of preserved material of *Ulva* revealed a feature which to my knowledge is not recorded in the literature. It was observed that certain cells or small groups of cells in areas well above the base of the frond may also send out descending rhizoids. The sections in question of Linnaeus's specimen thus probably came from a part of the thallus not too far removed from its base.

In his diagnosis of *U. lactuca*, Linnaeus (1753, p. 1163) referred to the thallus as palmate, which is not a feature of the plant that is currently known by this name. As the type specimen was not straightened when it was pressed, it was not possible to obtain a clear picture of its habit. At my request, Dr Metcalfe agreed to have the type soaked and straightened on the paper. Mrs Butler of the British Museum (Natural History) most thoughtfully wrote me about the appearance of the plant when soaked as follows:

> ...it is quite a large, healthy-looking specimen and we had no difficulty in soaking it out. It consists of very many fronds radiating from a central part; I am not very clear about the structure of this central part, my impression is that there were several points of attachment. We detached a group of fronds and re-mounted it at the side of the original specimen.
>
> The basal part of the plant divided up into many fronds. The basal part and the lower part of the frond seemed quite thick and fleshy, the edge of the lower part of the frond was dentate with quite large teeth. It was fairly narrow, sometimes had a darkish stripe up the middle and had a definite tendency to twist spirally. The terminal portion of the frond was

much thinner than the base and lower part and disintegrated a little as it was soaked out and moved. It was, I think, oval in shape with a smooth non-dentate margin.

The clear distinction between the different parts of the plant impressed me, it seemed very different from what I had envisaged as typical *U. lactuca* although I know how variable this plant can be.

The part of the type that was soaked and straightened is shown in Pl. **1**, fig. 10. It is evident that the plant is not typical of *U. lactuca* as currently accepted. It seemed likely that the species might be representative of *Monostroma.* Mrs Butler's remark that 'the terminal portion of the frond was much thinner than the base and lower part and disintegrated a little as it was soaked out and moved' suggested that the terminal part might be monostromatic. The possibility that *U. lactuca* was a species of *Monostroma* was further strengthened by the fact that the *Ulva lactuca* of many early authors was a species of *Monostroma*, *M. grevillei* (cf. Silva, 1952, p. 295). In fact, Kützing (1843) referred only monostromatic species to *Ulva*, and J. Agardh in 1883 formally removed *U. lactuca* to *Monostroma.*

At my further request, Dr Metcalfe agreed to have sections made through the terminal region of the type to determine whether or not the thallus is monostromatic in the distal region. The sections show that the specimen is distromatic throughout.[1] Hence, on the basis of the information now at hand, it must be concluded that *Ulva lactuca* is a species of *Ulva* in the current sense. But whether or not the type is an example of the taxon currently known by the name *U. lactuca* is a question which can only be settled by a study of the variability of this species throughout its range. In the *Species Plantarum*, Linnaeus gave the locality merely as 'in Oceano', whereas in the second edition of his *Flora Suecica*, he (1755, p. 433) gave as locality for *U. lactuca*: 'in Oceano Bahusiensi frequens'. This suggests that the type may have been obtained along the west coast of Sweden.

Another species of *Ulva* that has been the cause of considerable disagreement is *U. rigida*. This species was described by C. Agardh in 1822 (p. 410). He gave its distribution as the Atlantic Ocean as far south as the Cape of Good Hope, and the Mediterranean and Black Seas. Specifically, he listed only specimens given him by Desfontaines and Cabrera. Search in the Agardh Herbarium at Lund in 1940 was rewarded with the finding of an excellent specimen sent by Cabrera (one of two) which agrees well with C. Agardh's description of the species.

Since the material sent to C. Agardh by Cabrera invariably appears to have been collected at Cadiz (on the Atlantic coast of southern Spain), it is highly probable that the Cabrera specimens of *Ulva rigida* also had Cadiz as their source. I have chosen one of these specimens (Pl. **1**, fig. 11) as lectotype of *U. rigida*. Frequently *U. rigida* is regarded as the same as *U. lactuca* or it is considered a variety or forma of *U. lactuca*. On the basis of Cabrera's material I am inclined to consider *U. rigida*, in agreement with Feldmann (1937), as an autonomous species. The thallus is much more rigid and leathery than that of the plant currently known as *U. lactuca* (Text-fig. 3) and its cells as seen in section through the thallus are palisade-like and larger (Text-fig. 4).

Thuret (1854) specifically listed only three species as belonging to *Ulva*: *U. lactuca*, *U. rigida* and *U. linza*. In view of the uncertainty concerning the species represented by the type of *U. lactuca*, it seems best not to select this species as the type of *Ulva* Thuret. Furthermore, Thuret's concept of *U. lactuca* was based on a plant (see Thuret & Bornet, 1878, pl. 2) which although usually accepted (perhaps in error) as typical of *U. lactuca*, was recently considered by Føyn (1955) as representative of a distinct taxon, *U. thureti* Føyn. *U. linza* is placed in *Enteromorpha* by many authors (cf. Silva, 1952, p. 295) and would therefore be unsatisfactory as the type of *Ulva*. *Ulva* Thuret is thus best lectotypified by *U. rigida*.

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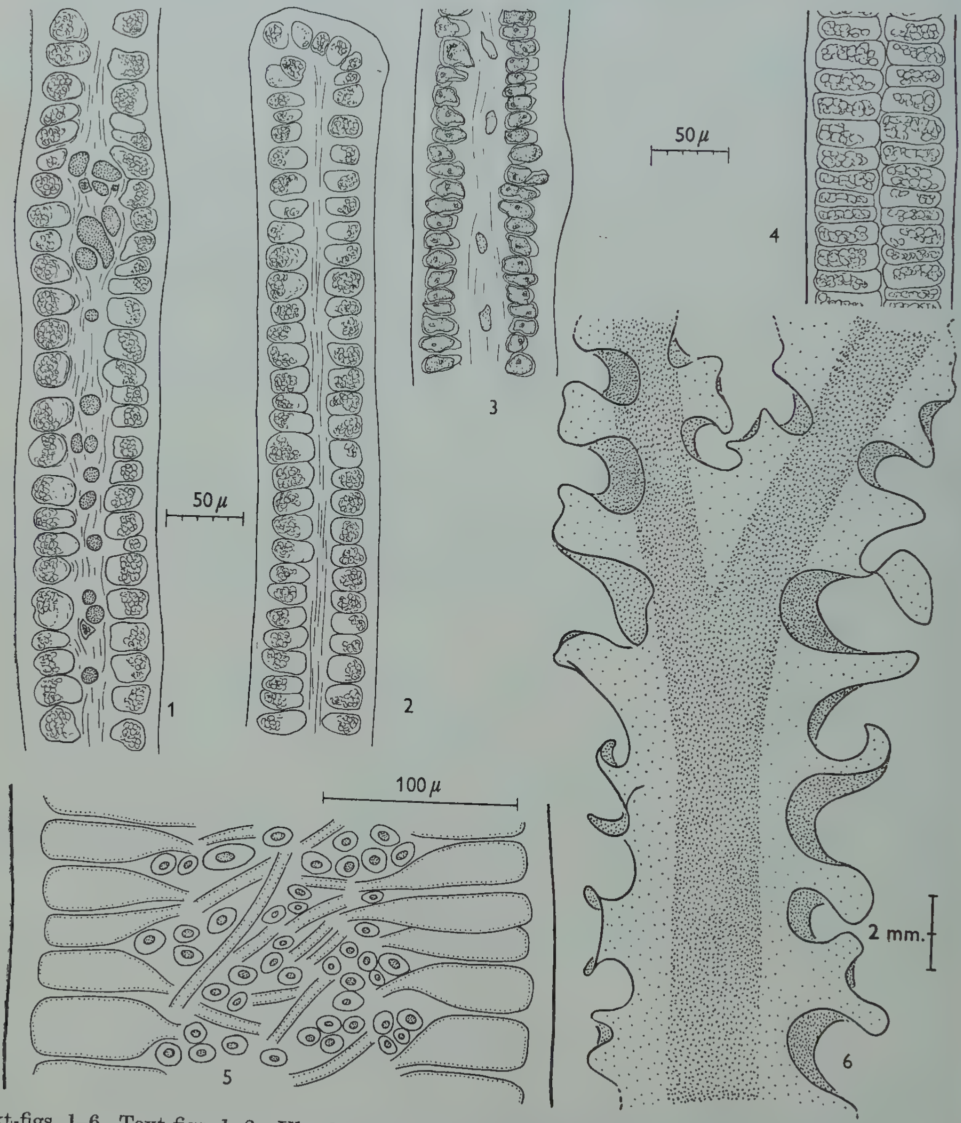
[1] The terminal region of the thallus is 25–50μ thick and the non-rhizoid-containing basal region is 75–90μ thick.

LETTERSTEDTIA

The genus *Letterstedtia* was erected by Areschoug (1851*a*) to receive a new species, *L. insignis*, material of which Letterstedt had collected in the vicinity of Port Natal (now Durban), South Africa, in 1846 and 1847. Before the turn of the century, two more species were added to the genus, namely, *L. petiolata* J. Agardh (1883) from Australia and *L. japonica* Holmes (1896) from Japan; and recently Chapman (1952) described two species from New Zealand, *L. stipitata* and *L. ulvoidea*.

Areschoug (1851*b*) placed *Letterstedtia* in the Ulvaceae and compared it with *Ulva*, with



Text-figs. 1–6. Text-figs. 1, 2. *Ulva lactuca* (Type)—sections through basal region of thallus. Text-fig. 3. *U. lactuca*: Varberg, Sweden, 8. iv. 1934, *Hylmö* (UC 531892)—section through basal region of thallus. Text-fig. 4. *U. rigida* (Lectotype)—section through thallus. Text-figs. 5, 6. *U. insignis*—text-fig. 5, section through part of axis with internal rhizoids; text-fig. 6, surface view of axis with internal rhizoids.

which he found it to agree anatomically in having a thallus that is distromatic, but to differ in habit in that the thallus is divided longitudinally into narrow and deep segments that produce lateral 'leaflets' in a more or less pinnate fashion.

Since the time of its founding, the autonomy of *Letterstedtia* has not been questioned. However, only J. Agardh (1883), Murray (1895) and West (1916), in addition to Areschoug, appear to have seen specimens of *L. insignis*, which not only is the type of the genus but its most distinctive species. All other accounts (De Toni, 1889; Wille, 1890; Oltmanns, 1904, 1922; Printz, 1927; Fritsch, 1935) are essentially based on Areschoug's statements and illustrations. And since these are not entirely accurate, the erroneous impression that *Letterstedtia* represents a distinctive type among the Ulvaceae has persisted.

A study of *L. insignis*, *L. petiolata* and *L. japonica*, and a comparison of them with representatives of *Ulva*, have convinced the writer that *Letterstedtia* is not sufficiently distinct from *Ulva* to warrant generic separation. The following comments are largely based upon an investigation of the South African *Letterstedtia insignis*, specimens of which were kindly furnished by Dr Mary A. Pocock. A brief abstract of the present account of *Letterstedtia* has been published (Papenfuss, 1954).

To judge from the accounts and illustrations of Areschoug, it would seem that *Letterstedtia* differs from *Ulva* principally in habit. Examination of Areschoug's original material revealed, however, that his specimens do not exactly agree with his diagnosis and illustration of the habit (Pl. **2**, fig. 12[1]) but agree with those collected in South Africa by the late Dr H. Becker (Pl. **2**, fig. 13) and Dr Pocock (Pl. **3**, fig. 14). None of the numerous specimens that I have seen shows the feature upon which Areschoug founded the genus, namely, the formation of determinate 'leaflets' in a more or less regular manner from both margins of the main axes. The plant illustrated by Murray (1895, p. 175, fig. 54) likewise lacked lateral appendages. (He thought that they had fallen off.) Pl. **2**, fig. 13 and Pl. **3**, fig. 14 show that the thallus is multifid and also that an occasional lateral proliferation may be formed. But these outgrowths are produced at irregular intervals and are much less pronounced than those shown by Areschoug.

Areschoug (1851*a*) also described and illustrated (Pl. **2**, fig. 12) a part of a young thallus of *Letterstedtia insignis*. This stage he depicted as consisting of narrow branches bearing lateral appendages that presumably mature into the 'leaflets' of determinate growth. Although very young thalli were not available for the present study, the early stages seen suggest that Areschoug's observations with respect to the juvenile thallus were also not entirely accurate. In the young condition (Pl. **3**, fig. 14) the thallus resembles that of a laciniate species of *Ulva*. The primary frond apparently splits lengthwise at an early stage into a number of segments that have their greatest width at the distal end. As growth advances the laciniae elongate and the broad tips undergo further lengthwise splitting and thus there is produced the multifid thallus characteristic of the adult plant (Pl. **2**, fig. 13). In older examples the main segments are somewhat cartilaginous and, as in certain species of *Ulva*, the margins become ruffled.

From J. Agardh's (1883) and Chapman's (1956) descriptions of *Letterstedtia petiolata* (Pl. **3**, fig. 15) and from the accounts and illustrations of *L. japonica* (Pl. **4**, figs. 16, 17) by Holmes (1896), Okamura (1928, 1936) and Chihara (1953), it is evident that the multifid condition of the thalli of these two species is likewise the result of repeated lengthwise splitting of the fronds. In habit, both *L. petiolata* and *L. japonica* resemble species of *Ulva* with lacerated fronds, except that in *L. petiolata* the proximal parts of the segments are narrow and stalk-like (Pl. **3**, fig. 15; see also Chapman, 1956, pl. 24).

Fertile areas were not observed in any of the specimens of *L. insignis* examined during the present study. According to Areschoug (1851*a*), reproductive bodies are produced in the cells of the lateral 'leaflets'. The only published information about the reproduction of *Letterstedtia* is that provided by Chihara (1953) with respect to *L. japonica*. He established that in this species, as in *Ulva*, the life history includes an alternation of isomorphic generations—the gametophytic plants are dioecious and produce biflagellate isogametes and the morphologically similar sporophytic plants form quadriflagellate zoospores.

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[1] This figure has been reproduced with slight alteration by Wille (1890, fig. 44 A), from whom it was copied by Printz (1927, fig. 127 A) and from whom it was taken in turn by Fritsch (1935, fig. 63 A).

Even though the distinctive features attributed to *Letterstedtia* by Areschoug are not entirely in accordance with the actual appearance of the plant, the unusual habit of *L. insignis* (as contrasted with that of some species of *Ulva* in which the thallus is more or less entire or broadly lobed or laciniate) may still suggest the desirability of maintaining the genus as an autonomous taxon. The differences between *Letterstedtia* and *Ulva* break down completely, however, if *Letterstedtia insignis* is compared with such transitional species as *Ulva schousboei* Bornet (1892, p. 194, pl. 1, figs. 2–3), *U. taeniata* (Setchell) Setchell & Gardner (1920*a*, p. 286, pl. 28; 1920*b*, pl. 23), *U. fasciata* Delile (1813, p. 297, pl. 58, fig. 5) and certain other species of *Ulva*.

The agreement in habit between *Letterstedtia insignis* (Pl. **2**, fig. 13; Pl. **3**, fig. 14) and *Ulva schousboei* (Pl. **4**, fig. 18) is specially striking, as was remarked upon by Bornet when he described the latter species. Passing from *U. schousboei* to such species as *U. taeniata* (Pl. **5**, fig. 19), *U. fasciata* (Pl. **5**, fig. 20), *U. dactylifera* (Setchell & Gardner, 1920*b*, pl. 21, fig. 1) and *U. stenophylla* (Setchell & Gardner, 1920*b*, pl. 24), it is seen that there is a transition from the very much dissected thallus typical of *Letterstedtia insignis*, *L. petiolata*, and *Ulva schousboei* to the undivided, elongate type of frond characteristic of *U. stenophylla* and certain other species of *Ulva*. In this connexion it is of interest also to note that Howe (1914, p. 20) considered *U. fasciata* f. *costata* as possibly representing a transitional type between *Ulva* and *Letterstedtia*. It is evident also that Chihara (1953, p. 199) was not satisfied with the assigning of *L. japonica* to *Letterstedtia* instead of *Ulva*, but in the absence of detailed information about the type species of *Letterstedtia* he justifiably refrained from transferring the Japanese species to *Ulva*.

In considering the possible autonomy of *Letterstedtia*, attention must be drawn also to an interesting anatomical feature noted by J. Agardh (1883) in *L. petiolata*, but not referred to by authors (with the exception of Chapman, 1952, p. 48; 1956) in later accounts of the genus. J. Agardh observed that in the basal petiole-like part of the segments of the thallus of this species, the cells produce hyphae that form a medulla-like layer similar to the layer of rhizoids produced from the cells at the base of the frond in species of *Ulva*. On account of this feature J. Agardh deemed it best to assign the Australian plant to *Letterstedtia* rather than *Ulva*, although not without some doubt, since a similar condition was not known to exist in *Letterstedtia insignis*.

It can now be reported that an internal layer of hyphae is likewise produced in the axes of *L. insignis*. The hyphae are formed by both cell layers (Text-fig. 5) in the axial region of the segments (Text-fig. 6) and cause the segments to be costate.

Similar hyphae were absent in sections made of the laciniae of *L. japonica*, but the limited herbarium material that was available for sectioning precludes the making of a positive statement as to their absence in this species. Neither Okamura (1928) nor Chihara (1953) mentions the occurrence of hyphae in the segments of *L. japonica*. On account of the presence of hyphae in the stipes, Chapman (1952, 1956) assigned to *Letterstedtia* two new species from New Zealand, *L. stipitata* and *L. ulvoidea*, but since all species of *Ulva* form hyphae in the basal part of the frond, there seems to be no reason for not placing them in *Ulva*.

Although the existence of transitional types between *Letterstedtia* and *Ulva* make it impossible to sharply delimit these two genera on the basis of habit, the presence of internal hyphae in parts of the frond distal to the basal stipe in both *Letterstedtia insignis* and *L. petiolata* raises the question whether the genus *Letterstedtia* ought to be maintained on the basis of this character.

To explore this possibility, sections were made of various species of *Ulva* to determine whether or not hyphae are formed in the frond. Although hyphae were never observed in the laciniae, it was found that they are frequently produced in the cartilaginous basal parts of the fronds and in some instances, as in certain examples of *U. fasciata* from Hawaii, the hyphae are formed in parts as much as 5 cm. above the holdfast. Hamel (1931, p. 138) also observed the presence of hyphae in this species in parts of the frond several centimetres above the holdfast, and Dangeard (1959, fig. 5) illustrates a plant with prominent costae in the laciniae, without stating, however, that the costae are formed by internal hyphae. It is evident, therefore, that in *Ulva* there are species in which hyphae are produced by parts distal to the basal holdfast. Hence, it is not possible to use this character as a clear-cut distinguishing feature between *Letterstedtia* and *Ulva*.

On the basis of the facts at hand, it thus appears there is no justification for maintaining *Letterstedtia* as a genus distinct from *Ulva*. The following species formerly ascribed to *Letterstedtia* should be referred to *Ulva*.[1]

Ulva insignis (J. E. Areschoug) Papenfuss, comb.nov. *Letterstedtia insignis* J. E. Areschoug, 1851*a*, p. 2, pl. 1. (Pl. **2**, fig. 13; Pl. **3**, fig. 14)

Type locality. Near Port Natal, South Africa.

Geogr. distr. Known only from South Africa.

Specimens examined. NATAL: near Port Natal (Durban), 1846–7, *Letterstedt* (Type material, S). CAPE PROVINCE: Waterloo Bay, 8. iv. 1944, *Pocock* 8047 (UC); Kleinmond (west of Great Fish River), 8. ii. 1947, *Pocock* 9116, 9117 (UC); Port Alfred, 24. ii. 1941, *Pocock* 4084, 4085, 4086, 4088 (UC); *Becker* (BOL, 28. vi. 1893; BM; UC, 10. vi. 1893); *Slavin* (BM); Port Elizabeth, *Weber–van Bosse* (L); comm. *Duthie* 8359 (UC).

Ulva japonica (Holmes) Papenfuss, comb.nov. *Letterstedtia japonica* Holmes, 1896, p. 250, pl. 7, figs. 3*a*–3*d*. (Pl. **4**, figs. 16, 17)

Type locality. Enoshima, Sagami.

Geogr. distr. Japan: east coast of central and southern Japan and west coast of Kyushu (Segawa, 1956), Amami Islands (Tanaka, 1956). China: Weihaiwei, Shantung Peninsula (Cotton, 1915).

Specimens examined. SAGAMI: Enoshima, iii. 1894, *Ohkubo* 40 (Type, BM); iv. 1898, Okamura's *Algae japonica exsiccatae* 45 (UC); 23. vi. 1923, *Yamada* (UC); iii. 1924, ex Herb. *Michitaro Higashi* (UC); Misaki, viii. 1906, ex Herb. *Yendo* (UC).

Ulva spathulata Papenfuss, nom.nov. *Letterstedtia petiolata* J. Agardh, 1883, p. 176. *Ulva petiolata* (J. Agardh) Womersley, 1956, p. 354 (non Turra, 1780, p. 68). (Pl. **3**, fig. 15)

Type locality. Port Phillip, Victoria, Australia (*vide* Womersley, *loc. cit.*).

Geogr. distr. Australia: New South Wales, Victoria, South Australia (*vide* Womersley, *loc cit.*) and Western Australia; New Zealand.

Specimens examined. SOUTH AUSTRALIA: Point Sinclair, 26 i. 1951, *Womersley* A 15225 (UC). WESTERN AUSTRALIA: Fremantle, 12. iv. 1927, *Setchell* (UC); Nov. Holl. part of a J. Agardh specimen obtained by Setchell from Herb. Kew (Isotype?, UC). NEW ZEALAND: Bluff (Ninety-Mile Beach), 18. i. 1941, *Lindauer* 2057 (UC).

MONOSTROMA

Monostroma Thuret (1854) is characterized by the monostromatic condition of the mature thallus. In some species the macroscopic plant represents the gametophytic generation, whereas in others it represents the sporophytic generation, and in species of the latter type a sexual generation appears to be lacking.

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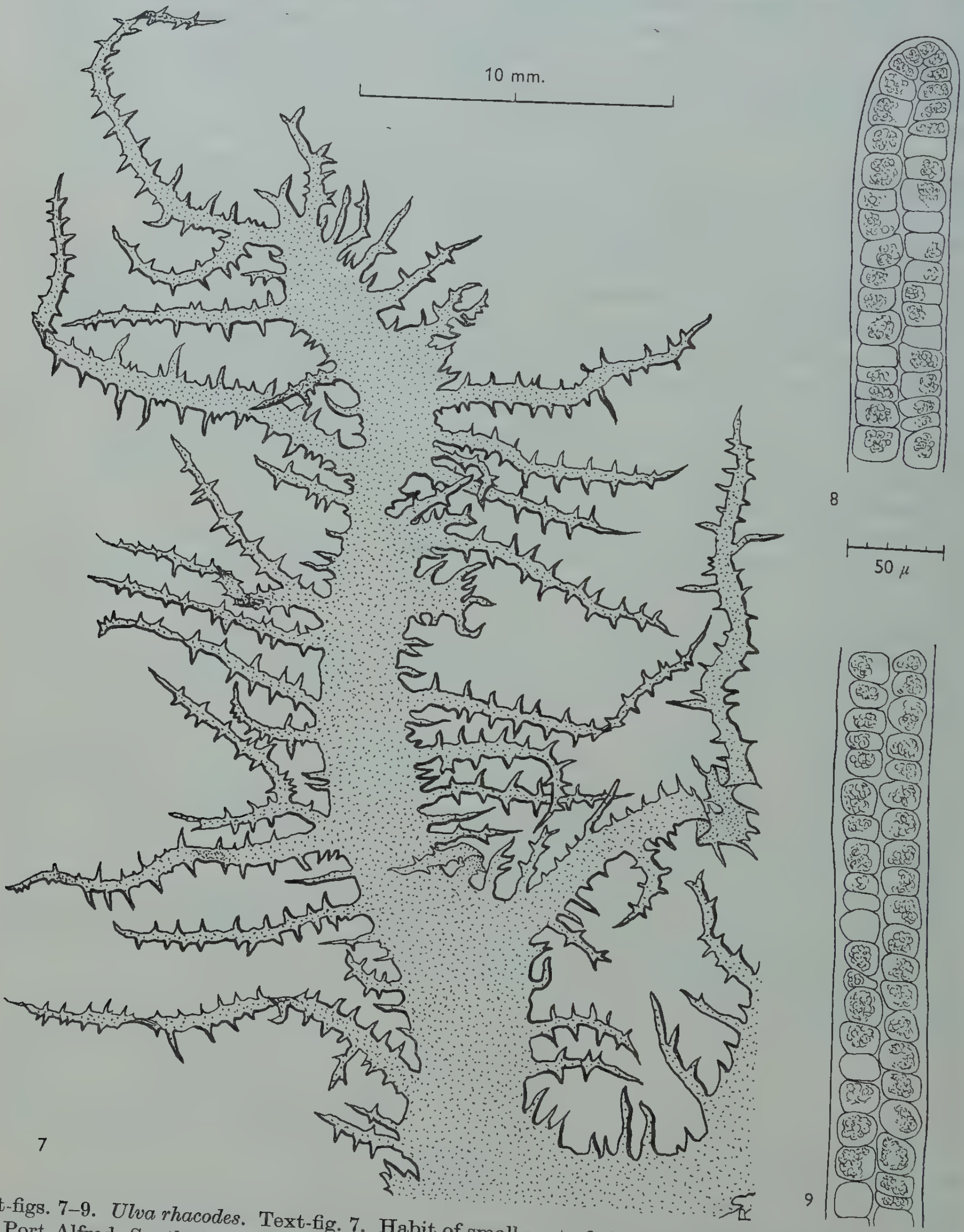
[1] Since the two species of *Letterstedtia, L. stipitata* and *L. ulvoidea*, described as new by Chapman (1952) are somewhat lacking in distinctive morphological characters, it seems best not to remove them to *Ulva* as autonomous taxa.

As regards the nomenclature of *Monostroma*, it might be noted that Kützing (1843 was the first to separate the monostromatic species of '*Ulva*' from the distromatic species Believing, in agreement with many other workers, that *U. lactuca* L. was based upon a monostromatic plant, he retained the name *Ulva* for the monostromatic species of the complex and proposed the name *Phycoseris* for the distromatic species. The name *Monostroma* is antedated, however, by *Ulvaria* Ruprecht (1851), which is based on two species, *Ulva splendens* Postels et Ruprecht and *Ulvaria fusca* Ruprecht. Authentic specimens of these species have been examined by Wittrock (1866) who found them to be mono-



Text-figs. 7–9. *Ulva rhacodes*. Text-fig. 7. Habit of small part of plant (formalin-preserved material: Port Alfred, South Africa, 2. vii. 1938, *Pocock & Papenfuss*). Text-figs. 8, 9. Sections through marginal and central regions of thallus, respectively.

stromatic. The two taxa have a wide distribution in the northern hemisphere. Rosenvinge (1893) regarded *Ulvaria splendens* as a variety of *U. fusca* and in this he has been followed by a number of workers. Dr A. D. Zinova has kindly sent me a fragment of one of Postels and Ruprecht's original specimens of *U. splendens* in the Leningrad Herbarium, examination of which has confirmed the observation by Wittrock that the plant is monostromatic.

In view of the more or less world-wide distribution of *Monostroma* and the frequent reference to it in floristic and morphological publications, it is proposed that this name be conserved against *Ulvaria*.

Enteromorpha

The nomenclatural history of *Enteromorpha* Link (1820) has been discussed by Silva (1952, pp. 294–7). The genus is characterized by the tubular thallus of the majority of species. In some forms, for example *E. linza*, only the stipe and the margins of the thallus may be hollow. These transitional species have been the cause of a great deal of disagreement as to their generic position in *Enteromorpha* or *Ulva* (cf. Silva, 1952, p. 295). It seems likely that an investigation of the ontogeny of the thallus of plants grown in culture may assist in determining the generic position of these partially hollow species. Doty (1947) distinguishes *Ulva* from *Enteromorpha* primarily on the basis that in *Ulva* the margin of the thallus is composed of about three cells, whereas in *Enteromorpha* it consists of more than three cells. This does not introduce a new character, however, because the greater width of the margin in *Enteromorpha* is the result of the hollow condition.

Holmes (1894) described a species from South Africa under the name *Enteromorpha rhacodes*. Examination of the type (BM) of this species (Pl. **6**, fig. 21) and of material of it collected at Port Alfred (Text-fig. 7), the type locality, by Dr M. A. Pocock and me has shown that the two layers of cells adhere to each other (Text-figs. 8, 9) and that the thallus does not at any stage become tubular. The plant thus represents a very distinctive species of *Ulva*: **Ulva rhacodes** (Holmes) Papenfuss, comb.nov. *Enteromorpha rhacodes* Holmes (1894, p. 89).

Percursaria

Some authors do not accept *Percursaria* Bory (1823) but merge it into *Enteromorpha*. In agreement with Rosenvinge (1893), Setchell & Gardner (1920*b*) Newton (1931), Kylin (1949), Kornmann (1956) and Taylor (1957), I regard the genus as distinct from *Enteromorpha*. The simple, non-tubular filaments, composed of two longitudinal series of cells, clearly distinguish *Percursaria percursa* from species of *Enteromorpha*. In this connexion, attention should be called to Kornmann's (1956) excellent account of the structure and reproduction of *Percursaria*.

Papenfuss (1950) proposed *Percursaria* Bory (1823) for conservation against *Percursaria* Bonnemaison (1822), a genus of blue-green algae, but Silva (1952) has pointed out that the latter name is invalid, since valid nomenclature of the groups of blue-green algae concerned does not begin until later. Hence, *Percursaria* Bory is not in need of conservation. If Silva's (1958, p. 184) proposal that later starting-points in the nomenclature of algae be abandoned is accepted by the Montreal or a subsequent Congress, the conservation of *Percursaria* Bory might be considered again.

Capsosiphon

Capsosiphon Gobi (1879) is generally regarded as an autonomous genus. In the possession of a tubular thallus, with the sides of the tube one cell-layer thick, it agrees with *Enteromorpha*. It differs from *Enteromorpha* especially by the fact that the thallus is gelatinous and that the cells occur in two's or four's, are enclosed within the wall of the mother cell, and are arranged in distinct loosely adherent longitudinal series. Bliding (1935) has shown that the genus lacks sexual reproduction and that reproduction is by quadriflagellate zoospores. Iwamoto (1959), however, reports only biflagellate reproductive cells, which he suspects of being gametes. For a long time the genus comprised only one species, but Chapman (1952) recently described a second species from New Zealand.

BLIDINGIA

Blidingia Kylin (1947), which is based on *Enteromorpha minima* Nägeli ex Kützing (1849, p. 482), is characterized by two features. Firstly, in its early stages of development, the plant consists of a prostrate system which becomes distromatic in the central region and later produces erect tubular fronds. Secondly, all the cytoplasm of the germinating zoospores migrates into the germ tube which is cut off by a transverse septum from the empty basal end. Reproduction is by quadriflagellate zoospores (Bliding, 1938).

Recently Dangeard (1958) transferred a second species of *Enteromorpha*, *E. marginata* J. Agardh, to *Blidingia*. It should be noted that in the method of germination of the zoospore, this species apparently differs from *B. minima* in that the basal cell of the sporeling is not empty.

RHIZENTERON

Rhizenteron P. Dangeard (1952*a*, *b*), which was based on two species, *R. tuberculosum* (P. Dangeard) P. Dangeard and *R. saxatile* P. Dangeard, is characterized by the fact that the rhizoids form a basal tubercle or shrub-like growth, from which issue weakly developed, tubular, free fronds. The sides of the tubular fronds are, as in *Enteromorpha*, one cell-layer thick. *R. tuberculosum* is here designated as lectotype of the genus.

LOBATA

Chapman (1952, p. 48; 1956) distinguished his genus *Lobata* from *Ulva* essentially on the basis of 'reproductive bodies produced in certain cells of [the] axis portion' of the frond. However, the true nature of these presumed reproductive bodies remains to be determined. It is not inconceivable that they represent rhizoidal cells filled with storage products or possibly an endophyte. Also, on strictly technical grounds *Lobata* is still invalid, since the 'reproductive bodies' have not as yet been observed in the species that was designated as the type of the genus, *L. phyllosa*. This species is therefore transferred to *Ulva* as **Ulva phyllosa** (Chapman) Papenfuss, comb.nov. *Lobata phyllosa* Chapman (1952, p. 49, fig. 3, pl. 21).

GEMINA

Chapman (1952, p. 51; 1956) separates his genus *Gemina* from *Enteromorpha* and *Ulva* primarily by the fact that it produces 'reproductive bodies in special cells at [the] base of [the] thallus'. Since it is not yet certain that these cells actually are reproductive cells (those illustrated in *Gemina linzoidea* strongly resemble rhizoidal cells that are filled with storage products) and inasmuch as they are not known to occur in the species that was designated as the type of the genus, *G. enteromorphoidea*, it seems best to consider *Gemina*, at least as regards the type species (which is fistular), as congeneric with *Enteromorpha*. Some of the species assigned to *Gemina* by Chapman may be representative of *Ulva*, to judge from his descriptions and illustrations. Since the five species accredited to *Gemina* by Chapman are lacking in distinctive morphological characters, it seems best not to transfer them to *Ulva* or *Enteromorpha* at this time.

FELDMANNODORA

Feldmannodora Chadefaud (1957) is a monotypic genus based upon *Enteromorpha chadefaudii* Feldmann. In habit this genus resembles *Enteromorpha*, but it differs from the latter especially in its possession of stellate plastids, with the arms of the star extending from the terminal end of the cell (at the surface of the thallus) to the base of the cell, and in the disposition of the cells in the adult fronds in dendroid systems, each enclosed in its own sheath.

In connexion with *Feldmannodora*, it should be pointed out that Jane & Woodhead (1941) have observed that under certain conditions the cells of *Ulothrix* form a thick sheath. They regard this condition as perhaps pathological. Whether the production of a sheath by the cells of *Feldmannodora* is conditioned by the relatively dry habitat of this plant is not known but it would be of interest to make observations on the cell walls of plants grown in liquid medium.

For a long time all members of this complex were placed in the family Ulvaceae Lamouroux orth. mut. Dumortier (1822, p. 72). In recent times separate families have been established for *Monostroma* and *Capsosiphon*.

Kunieda (1934) suggested that, on the basis of its deviating life history, *Monostroma* be removed from the Ulvaceae to a family Monostromaceae. Suneson (1947) was the first, however, to formally recognize the Monostromaceae. Kylin in 1947 removed the family from the Ulvales to the Ulotrichales but later (1949) returned it to the Ulvales.

It is not inconceivable that when more is known about the developmental morphology of this assemblage of algae, it will be found that the Monostromaceae cannot be maintained. For the present, it seems desirable, however, to recognize the distinctive features of *Monostroma*, as contrasted with other Ulvales, and to accord it family status.

There are some characters shared by certain species of *Monostroma* and *Blidingia minima* which suggest a closer relationship between these genera than has been generally recognized, but we need to know more about the developmental history of the various species of *Monostroma* before definite conclusions can be drawn on this point. In *Blidingia minima* the cytoplasm migrates into the terminal end of the one-celled sporeling (germinating zoospore) which is cut off by a transverse septum from the proximal empty end (Bliding, 1938, figs. 2*g*–*i*; Yamada & Kanda, 1941, figs. 5E–L, 6I). The same method of germination has been observed in the zoospores of *M. pulchrum* (Yamada & Saito, 1938, figs. 12D–E) and in the zygotes of *M. angicava* (Yamada & Saito, 1938, fig. 9I), *M. grevillei* (Schreiber, 1942, figs. 1*f*–*g*) and *M. latissimum* (Carter, 1926, figs. 63, 65).

In *Blidingia*, the early stages of the thallus are in the form of a prostrate disk (Bliding, 1938; Yamada & Kanda, 1941). In *Monostroma angicava* the zoospores produced in the cysts likewise give rise to a prostrate growth (Yamada & Saito, 1938), but the most striking correspondence is with *M. zostericola* in which the macroscopic plant represents (as in *Blidingia*) the sporophytic generation and its zoospores produce discoid growths similar to those of *Blidingia* (Yamada & Kanda, 1941).

Although *Capsosiphon* differs strikingly from other genera of the Ulvales, there appears to exist no adequate basis, at present, for removing it to a separate family, Capsosiphonaceae, as Chapman (1952) has proposed. Chapman's statement that reproduction in *Capsosiphon* is by aplanospores fails to take account of the observations of Bliding (1935), who found that reproduction is exclusively by quadriflagellate zoospores. As has already been remarked, Iwamoto (1959) recently also reported biflagellate reproductive cells.

Finally, it may be desirable to consider briefly the question whether or not the Ulvales merit ordinal rank. Blackman & Tansley (1902) removed the Ulvaceae from the Ulotrichales of Borzi (1895) and elevated them to the rank of order on account of their parenchymatous thallus, as contrasted with the filamentous condition of typical Ulotrichales. Although a few early authors (e.g. West, 1904, 1916) accepted the classification of Blackman & Tansley, wide recognition of the order did not come until comparatively recently. This recognition was especially influenced by the discovery by Hartman (1929), Kylin (1931), Føyn (1934) and many other investigators that the life cycle of some species of *Ulva* and *Enteromorpha* includes an alternation of isomorphic generations and thus seemingly differs from that of the Ulotrichales. It is now reasonably well established, however, that some Ulotrichales (e.g. *Fritschiella* (Singh, 1947); *Draparnaldiopsis* (Singh, 1945)) also show an alternation of isomorphic generations. Furthermore, some of them are parenchymatous (e.g. *Fritschiella*) or show a tendency in this direction (e.g. *Stigeoclonium variabile* and *Draparnaldia glomerata* (Gay, 1891, pl. 8, figs. 68–72, and pl. 10, fig. 95, respectively)). The sporeling (filamentous) stages of *Ulva* and *Enteromorpha* and the young, uniseriate, branches of *Enteromorpha* also show a striking resemblance to filaments of *Ulothrix*. There thus appears to be a great deal of justification for the view of Fritsch (1935, 1944) that the Ulvaceae should be considered advanced Ulotrichales.

A synopsis of the genera comprising the Ulvaceae and Monostromaceae follows:

ULOTRICHALES BORZI (1895, p. 348)

Ulvaceae Lamouroux orth. mut. Dumortier (1822, p. 72)

Ulva Thuret, *Mém. Soc. Sci. Nat. Cherbourg* **2**, 28, 1854 (*nomen genericum conservandum propositum*). Species lectotypica: *U. rigida* [C. Agardh] Thuret. *Nomina generica rejicienda proposita*: *Ulva* Linnaeus, *Sp. Pl.* **2**, 1163, 1753. Species lectotypica: *U. intestinalis* Linnaeus. *Ramularia* Roussel, *Fl. Calv.* ed. 2, 98, 1806. Species lectotypica: *Ulva lactuca* Linnaeus (*vide* C. Agardh, *Sp. Alg.* **1** (2), 402, 1822). *Phycoseris* Kützing, *Phyc. Gen.* p. 296, 1843. Species lectotypica: *P. rigida* (C. Agardh) Kützing. *Letterstedtia* J. E. Areschoug, *Öfvers. K.* [*Sv.*] *Vet.-Akad. Förh.* 1850 (1), **2**, 1851. Species typica: *L. insignis* J. E. Areschoug.

Other synonym: *Lobata* Chapman, *Trans. R. Soc. N.Z.* **80**, 48, 1952. Species typica: *L. phyllosa* Chapman.

Enteromorpha Link in C. G. Nees, *Hor. Phys. Berol.* 5, 1820 (*nom. cons.*). Species lectotypica: *Ulva intestinalis* Linnaeus (*vide* Silva, 1952, p. 294). *Ulva* Linnaeus, *Sp. Pl.* **2**, 1163, 1753. Species lectotypica: *U. intestinalis* Linnaeus. *Splachnon* Adanson, *Fam.* **2**, 13, 1763. Species lectotypica: *Ulva intestinalis* Linnaeus (*vide* Silva, 1952, p. 294). *Solenia* (C. Agardh) C. Agardh, *Syst. Alg.* xxxii, 185, 1824 (non Hoffmann 1795). Species lectotypica: *S. intestinalis* (Linnaeus) C. Agardh. *Ilea* E. M. Fries, *Syst. Orb. Veg.*, 336, 1825. Species lectotypica: *Solenia intestinalis* (Linnaeus) C. Agardh. *Tubularia* Roussel, *Fl. Calv.* ed. 2, p. 98, 1806. Species lectotypica: *Ulva intestinalis* Linnaeus (*vide* Silva, 1952, p. 296). *Fistularia* Greville, *Fl. edin.* lxvi, 300, 1824 (non Stackhouse, 1816). Species lectotypica: *F. intestinalis* (Linnaeus) Greville (*vide* Silva, 1952, p. 297). *Hydrosolen* Martius, *Fl. Bras.* **1**, 10, 1833. Species lectotypica: *H. intestinalis* (Linnaeus) Martius (*vide* Silva, 1952, p. 297). *Kallonema* Dickie, *J. Linn. Soc. Bot.* **11**, 457, 1871. Species lectotypica: *K. ralfsii* (Harvey) Dickie. *Gemina* Chapman, *Trans. R. Soc. N.Z.*, **80**, 51, 1952. Species typica: *G. enteromorphoidea* Chapman.

Percursaria Bory, *Dict. Class. Hist. Nat.* **4**, 393, 1823. Species typica: *P. percursa* (C. Agardh) Bory. *Zignoa* Trevisan, *Prosp. Fl. Eug.* **50**, 1842. Species lectotypica: *Ulva percursa* (C. Agardh) C. Agardh. *Tetranema* J. E. Areschoug, *Nova Acta Reg. Soc. Sci. Upsal.* ser. 2, **14**, 418, 1850 (non *Tetranema* Bentham 1843, *nom. cons.*). Species typica: *T. percursum* (C. Agardh) J. E. Areschoug. *Diplonema* Kjellman, *K. Svensk. Vet.-Akad. Handl.* ser. 4, **20** (5), 302, 1883 (nec G. Don 1838 non De Notaris 1846). Species typica: *D. percursum* (C. Agardh) Kjellman.

Capsosiphon Gobi, *Trudy Leningrad. Obshch. Est.* **10** (2), 88, 1879. Species typica: *C. aureolum* (C. Agardh) Gobi (= *C. fulvescens* (C. Agardh) Setchell et Gardner). *Ilea* J. Agardh, *Lunds Univ. Årsskr. Avd.* **4**, 19 (2), 114, 1883 (non E. M. Fries 1825). Species typica: *I. fulvescens* (C. Agardh) J. Agardh.

Blidingia Kylin, *K. Fysiogr. Sällskap. Lund Förhandl.* **17** (17), 8, 1947. Species typica: *B. minima* (Nägeli ex Kützing) Kylin.

Rhizenteron P. Dangeard, *C.R. Acad. Sci.* [*Paris*], **235**, 1267, 1952. Species lectotypica: *R. tuberculosum* (P. Dangeard) P. Dangeard.

Feldmannodora Chadefaud, *Rev. Gen. Bot.* **64**, 668, 1957. Species typica: *F. chadefaudii* (J. Feldmann) Chadefaud.

Monostromaceae Kunieda ex Suneson (1947, p. 245)

Monostroma Thuret, *Mém. Soc. Sci. Nat. Cherbourg*, **2**, 29, 1854 (*nomen genericum conservandum propositum*). Species lectotypica: *M. oxycoccum* (Kützing) Thuret *nom. illeg. pro. M. oxyspermum* (Kützing) Doty. *Nomen genericum rejiciendum propositum*: *Ulvaria* Ruprecht in Middendorff, *Sibirische Reise, Bot.* **1** (2), 410, 1851. Species lectotypica: *Ulva fusca* Postels et Ruprecht (= *Monostroma fuscum* (Postels et Ruprecht) Wittrock).

Addendum

After this article had been submitted for publication, an extensive paper by Dr Mary A. Pocock on the structure and reproduction of *Letterstedtia insignis* appeared in *Hydrobiologia* (**14**, October 1959). Dr Pocock produces evidence for the maintenance of *Letterstedtia* as a distinct genus. The most important feature brought to light, in my opinion, is that trabecula-like cross struts are formed between the cells of the two layers in the costae of the laciniae. Whether or not similar trabeculae are produced in the costate or partially costate examples of *Ulva fasciata* remains to be determined. In view of the existence of transitional types between *Ulva* and *Letterstedtia*, as described in the present article, it still seems better to me to regard these two taxa as representing the same genus.

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EXPLANATION OF PLATES 1 TO 6

PLATE 1

Fig. 10. *Ulva lactuca* (part of Type, LINN). Fig. 11. *U. rigida* (Lectotype, LD).

PLATE 2

Figs. 12, 13. *Ulva insignis.* Fig. 12. Photograph of Areschoug's (1851 *a*) plate illustrating the species. Fig. 13. Habit of plant: Port Alfred, South Africa, 10. vi. 1893. *Becker* (UC), *ca.* 2/5 nat. size.

PLATE 3

Fig. 14. *Ulva insignis,* habit of immature plant: Waterloo Bay, South Africa, 8. iv. 1944, *Pocock* 8047 (UC). Fig. 15. *U. spathulata,* habit of plant: Point Sinclair, South Australia, 26. i. 1951, *Womersley* A 15225 (UC).

PLATE 4

Figs. 16, 17. *Ulva japonica*, habit of plant, original material of Holmes: Enoshima, Sagami, iii. 1894, *Ohkubo* 40 (BM). Fig. 18. *U. schousboe*, photograph of Schousboe's drawing of the species, published by Hamel (1931).

PLATE 5

Fig. 19. *Ulva taeniata,* habit of much segmented plant: near Piedras Blancas Point, San Luis Obispo County, California, 31. iii. 1947, *Silva* 1328 (UC). Fig. 20. *U. fasciata,* habit of plant: Waikiki, Oahu, Hawaiian Islands, 2. v. 1942, *Papenfuss* (UC).

PLATE 6

Fig. 21. *Ulva rhacodes* (Type, BM): Port Alfred, South Africa, 1893, *Becker*.

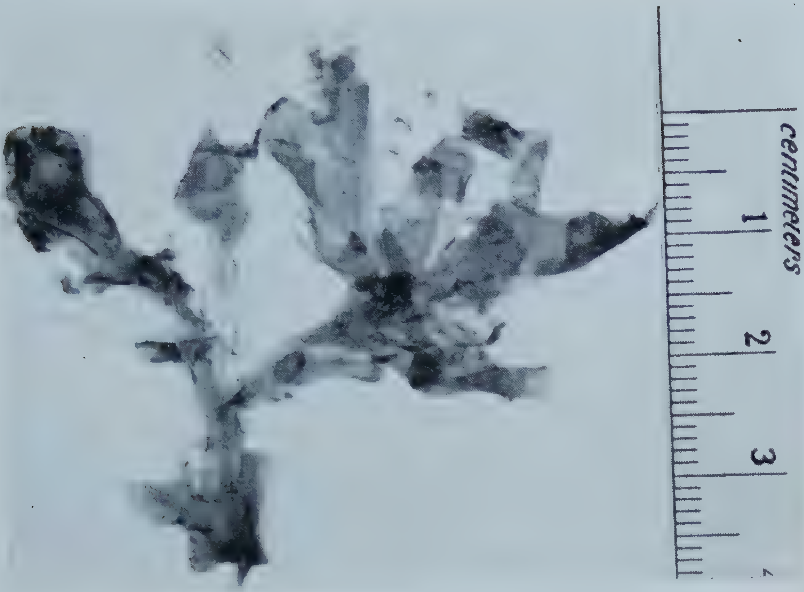

Fig. 10

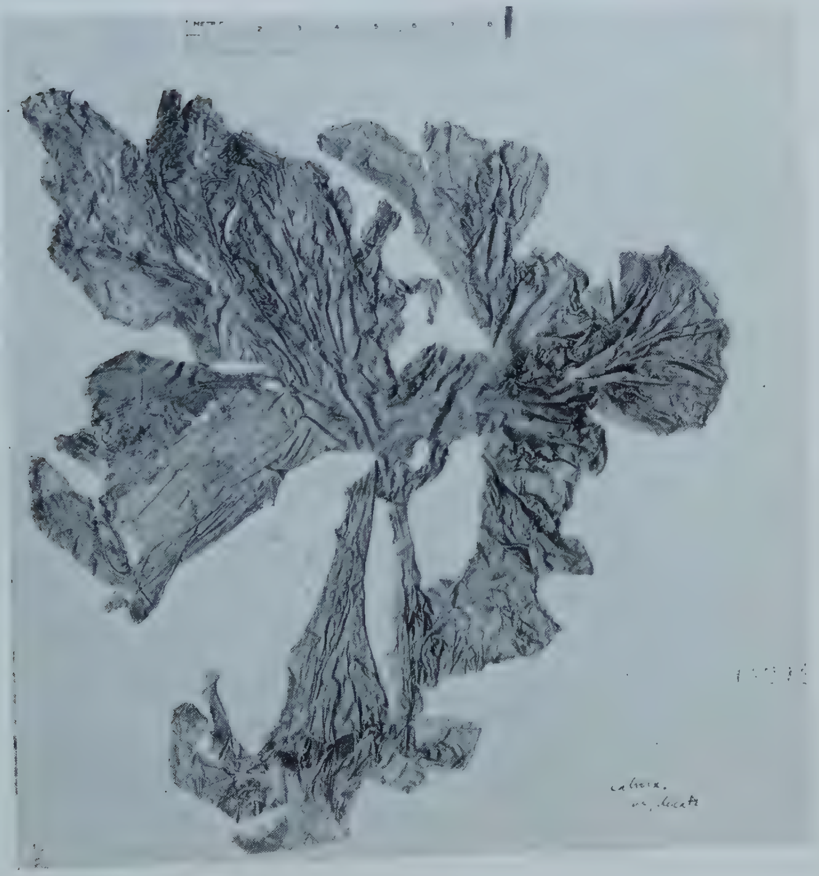

Fig. 11

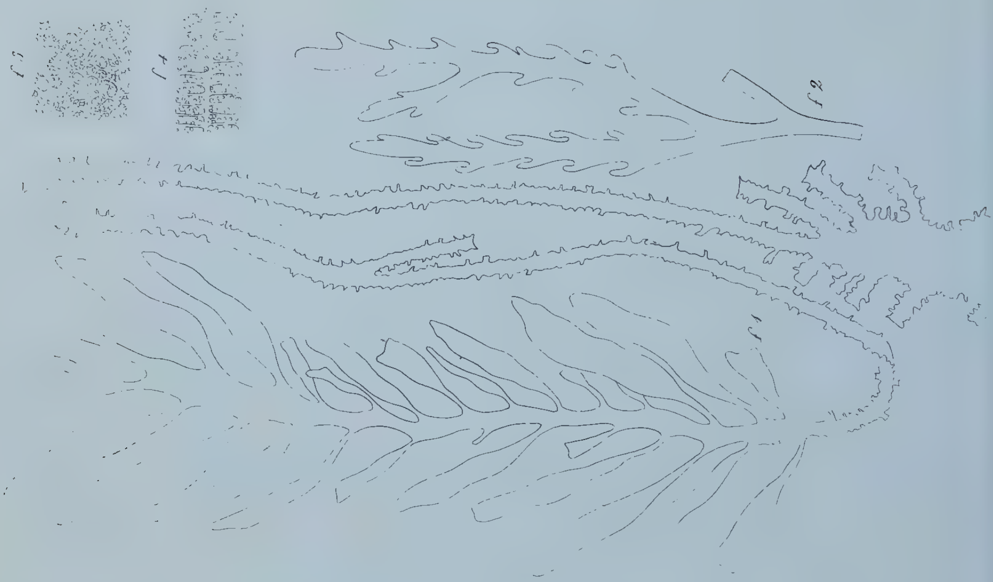

Fig. 12

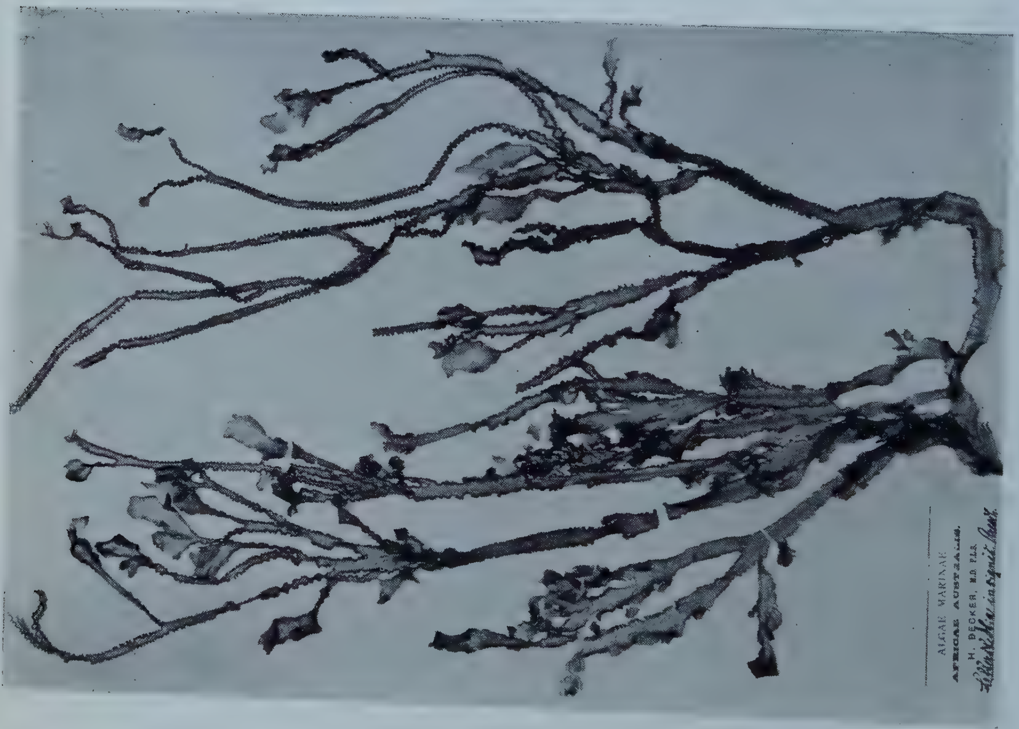

Fig. 13

G. F. PAPENFUSS

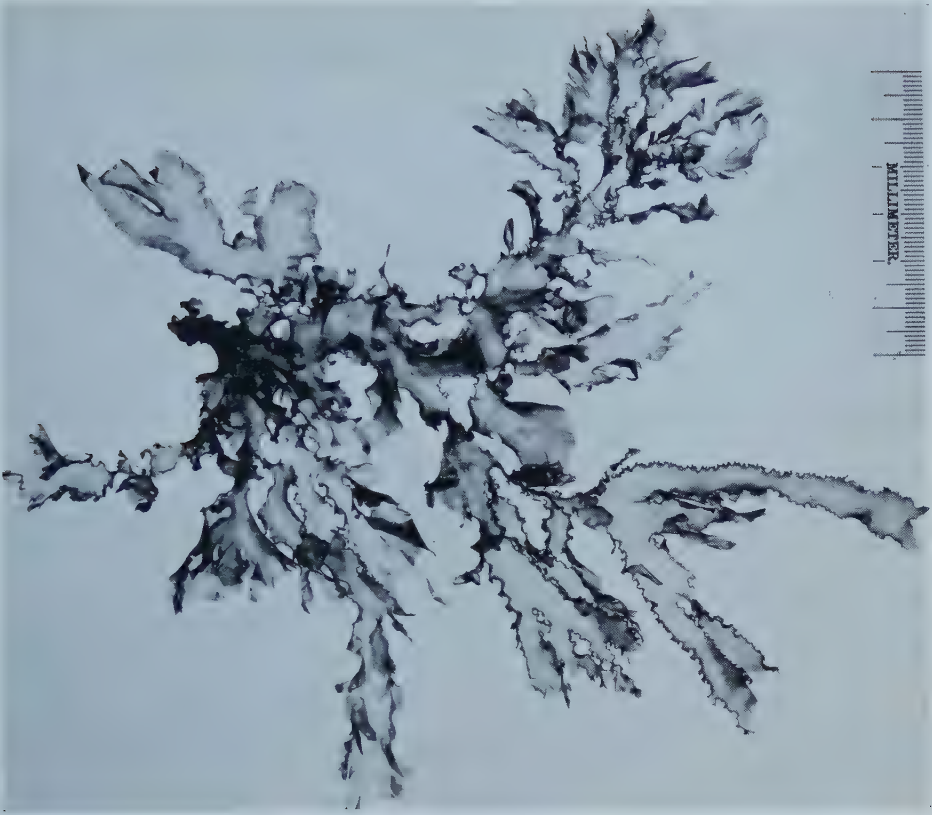

Fig. 14

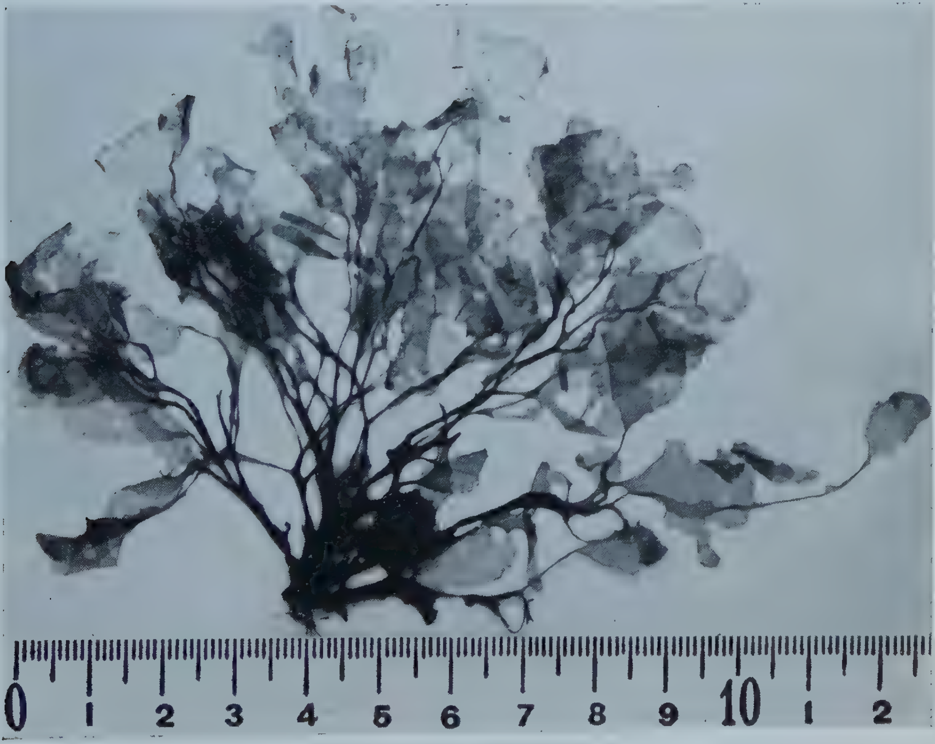

Fig. 15

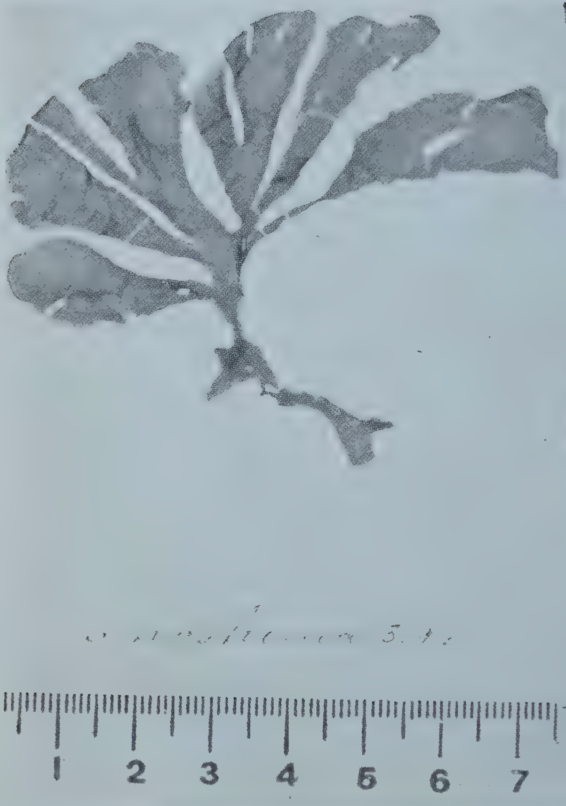

Fig. 16

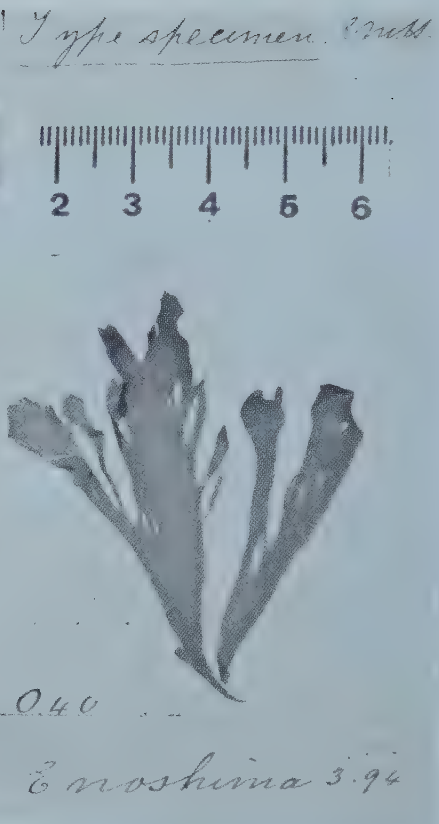

Fig. 17

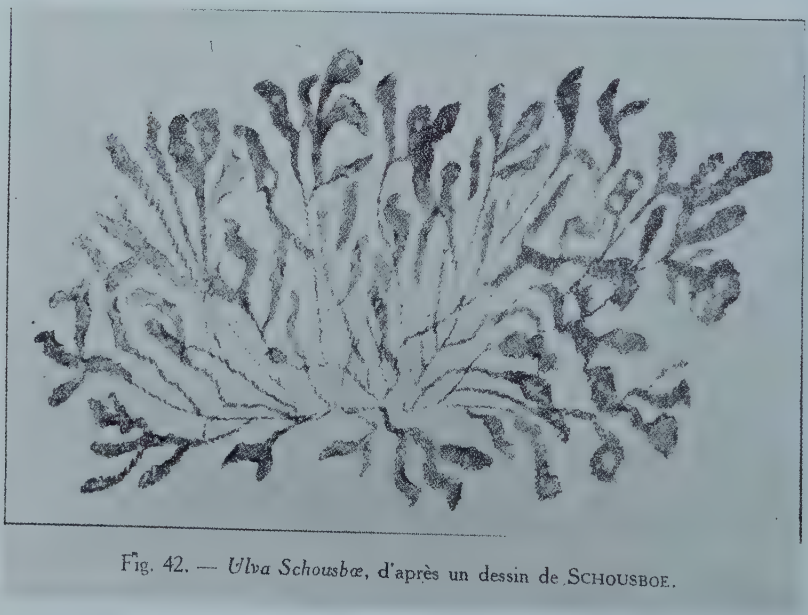

Fig. 42. — *Ulva Schousbœ*, d'après un dessin de Schousboe.

Fig. 18

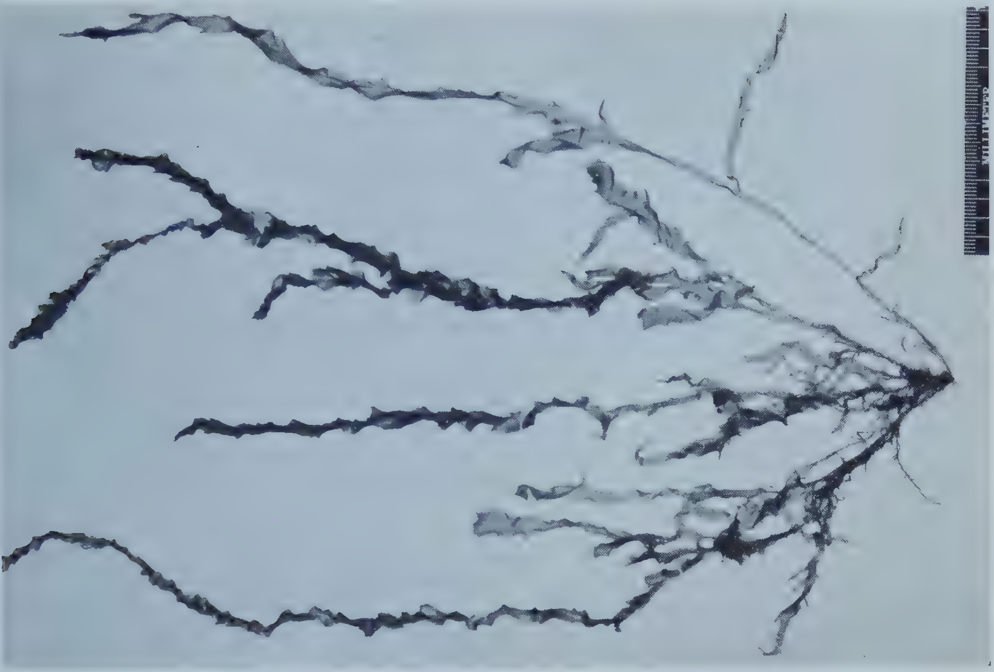

Fig. 19

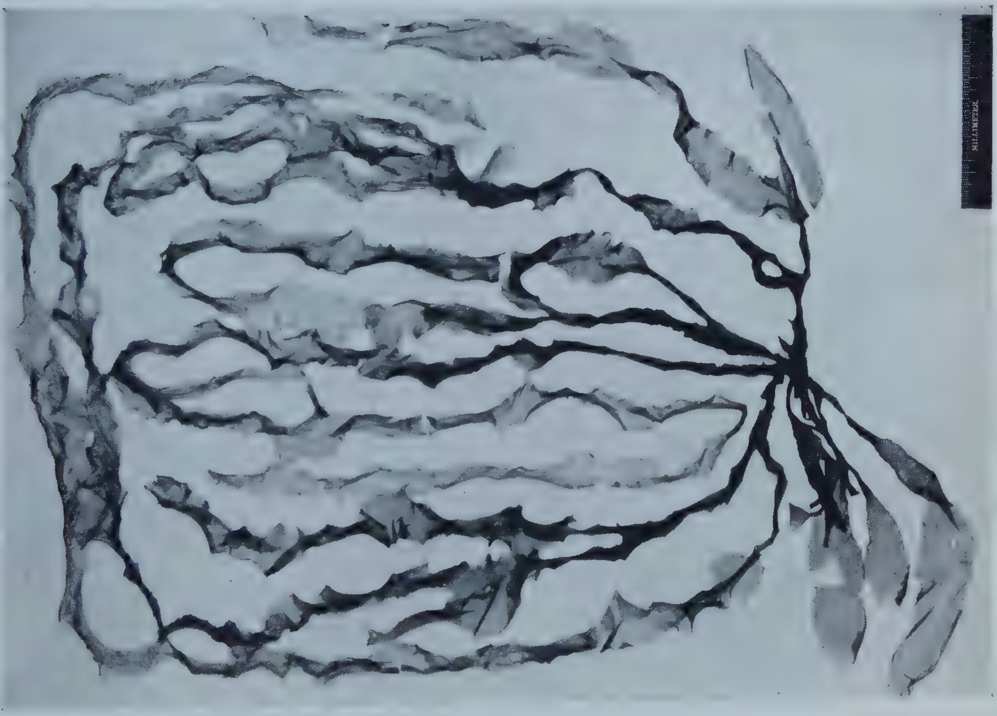

Fig. 20

G. F. PAPENFUSS

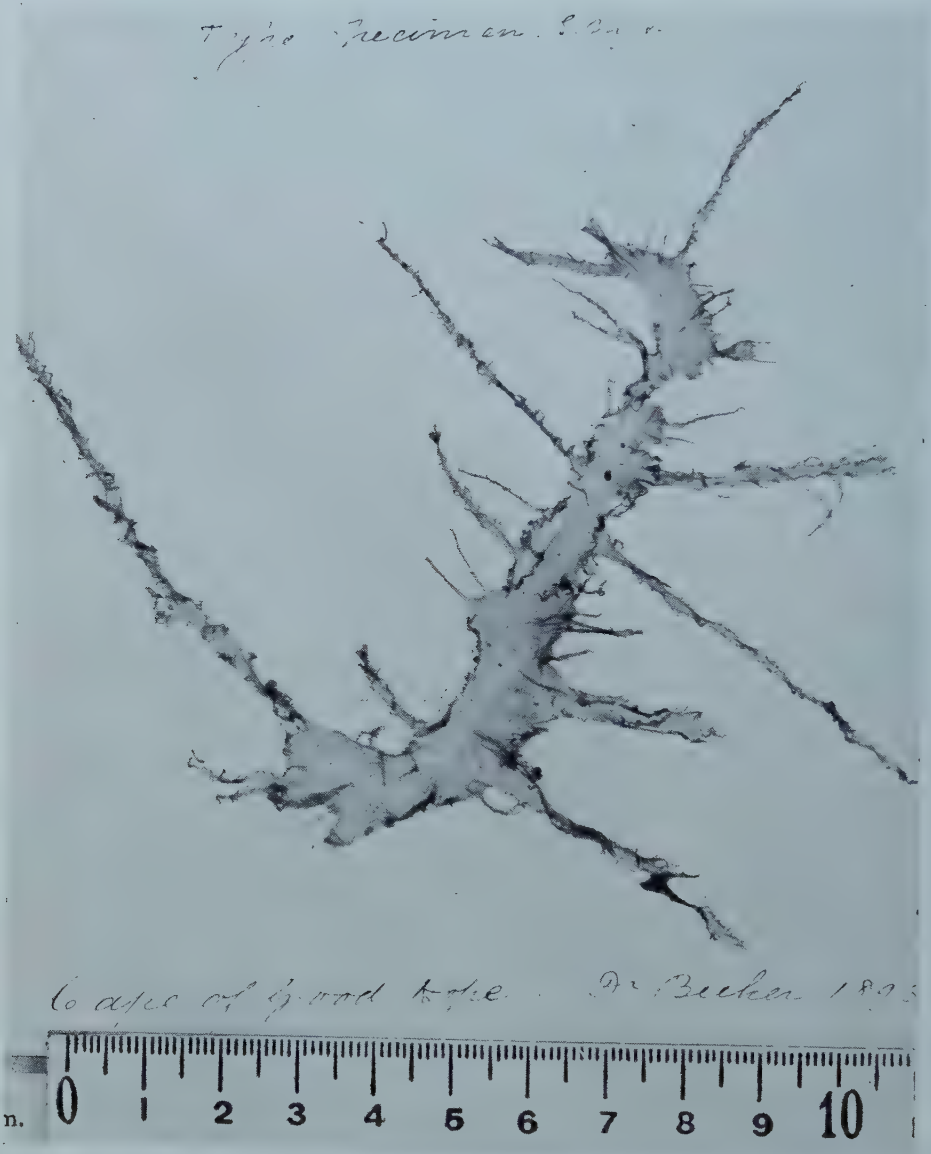

Fig. 21

J. Linn. Soc. (Bot.), **56**, **367**, *p.* 319
With 59 *text-figures*
Printed in Great Britain

The organography and the evolution of Dioscoreaceae, the family of the Yams

By I. H. BURKILL, F.L.S.

Liliales or, as some prefer, Liliiflorae, is a taxonomic concept covering the following families: Liliaceae, Juncaceae, Haemodoraceae, Amaryllidaceae, Iridaceae, Velloziaceae, Stemonaceae, Taccaceae and Dioscoreaceae. When first devised it was but a lexicographical convention; but with the advent of evolutionary ideas it came to imply important relations; and then to fill the time-scale, such terms as proto-Liliales and proto-Dioscoreaceae were added. This paper attempts to detect the course by which the proto-Liliales gave origin to the Dioscoreaceae through a postulate—proto-Dioscoreaceae. The writer, over many years, has used such means of study of the Dioscoreaceae in life as came to him, and part of the work done was published in the *J. Linn. Soc.* (*Bot.*), **53**, 313–82; 1949); this paper carries the work forward. Its purpose is phylogenetic; and as phylogeny is speculative, it is essential that it be reasoned and critical of the state of the taxonomy.

The recognition of the Dioscoreaceae as a natural family is the subject of the first pages (pp. 319–20); followed by some criticisms made in an effort to throw a boundary round the family. A German school of botanists declares that the family's closest affinity is with the Amaryllidaceae; this is contested (p. 320 and again on p. 335) where the tribe Asparagoideae of the Liliaceae is preferred. On p. 323 an attempt is made to show that there is compactness enough in the family, as here defined, to support the proposition that the proto-Dioscoreaceae left the rest of the proto-Liliales by a single exodus from a satisfactorily straightforward genesis. The link with the proto-Liliales, that is to say the proto-Dioscoreaceae, is regarded as of lowly herbs which adopted twining on the stems of woody Angiosperms as their means of attaining light without abandoning positions affording shelter when the weather turned against them. To understand the exodus the allied Liliales—Stemonaceae and Taccaceae as well as the Asparagoid Liliales—are examined in some detail on p. 345–49. Under § 10 (p. 343) geological history is brought in. It is thought that the remotest beginnings may have been in the Far East (p. 339). There is no evidence that the proto-Dioscoreaceae succeeded in spreading far, but reason for thinking that in time a line well fitted to exist—the Dioscoreaceae—spread west, and that the family as known today took its more or less pantropic modern existence from this line. The oldest irrefutable demonstration of the course of the Dioscoreaceae is that they were present and well diversified in the part of the southern World where the Atlantic rifted in the end of the Cretaceous. Not a single shaft of light has shown their earlier, but certain, existence.

At the end of the paper, after the different parts of the plant have been subjected to a morphological examination, a key is ventured (p. 402) for the sections in the Old World. It has not been possible to include the sections in the New World, for our knowledge of them in life is exceedingly poor. It will be for another botanist to supply a knowledge and to put into place their sections.

About 150 species of the family are cited by name. As the taxonomy is in an unsatisfactory state the species are listed (p. 408) with the necessary corrections.

An advantage follows, namely the elimination of author's names from the text. The reader's attention is sought for certain morphological observations which bear on general principles. The relatively abrupt appearance of decussate foliage in *Dioscorea* is regarded as made possible by sliding growth (p. 366), but invites study. The plagiotropic determination of internodal length, exposed already in the previous paper, receives (p. 362) further illustration. A rotation of the stem on its own axis (see p. 344 and 353) needs connecting with the initiation of a genetic spiral. The evolution of the nodal ganglion requires parallel studies in the Liliaceae, and so does the assembly of the primary nerves at the upper pulvinus.

The difference between the up-spiral and down-spiral sides of a leaf trace is noticed on p. 359.

I. TAXONOMY

§1. *The recognition of the Dioscoreaceae*

The recognition of the Dioscoreaceae as a family was due to R. Brown who, in 1819, associated together the genera *Dioscorea*, *Rajania* and *Tamus*, using Dioscoreae—the plural of the generic name—to embrace the three (*Prod. Fl. Nov. Holl.* **1**, 294). Because the use of a generic name in the plural in this way has great inconveniences in Latin diagnoses, Lindley substituted Dioscoreaceae; but that was not until 1836.

Antoine-Laurent de Jussieu, of the generation before R. Brown, had associated the same three genera with various genera of the Liliaceae, calling his assemblage Asparagi, using the generic *Asparagus* after the manner of R. Brown's Dioscoreae. He had not advanced in diagnosis so far as Brown did later.

Earlier (1788) a dried specimen of a very curious plant from Ceylon had reached J. Gaertner, who, to distinguish it, created the genus *Trichopus*, and called the species *T. zeylanicus*. It is a lowly plant. No one of the time was in the least likely to bring it alongside the climbing Dioscoreaceae which were then known; and no one did.

In 1832 Lindley assigned it to the Aristolochiaceae (*Bot. Reg.* pl. 1545). In 1859 Klotzsch removed it to the Dioscoreaceae. To do so he had to extend the boundary of the family in two respects, as it had hermaphrodite flowers and it did not climb.

In 1832, or 27 years earlier, Planchon had described as of a new genus the Philippine *Stenomeris dioscoreifolia*, putting it into the Burmanniaceae. He was led to this because he saw the flower to be like that of a newly discovered *Thismia*. In 1870 Beccari brought it into the Dioscoreaceae (*Nuov. Giorn. Bot. Ital.* **2**, 13), and consented to Klotzsch's transfer of *Trichopus*. He, to do this, had to break through the Dioscoreaceous character of 'two seeds in a loculus', for *Stenomeris* has many seeds in a loculus.

Fifty more years passed before Perrier de la Bâthie defined the Madagascan genus *Avetra*,[1] placing it in the position to which it manifestly belongs, namely next to *Trichopus*.

Avetra has a samara: then so has *Rajania*; therefore the differences between it and the well-known genera did not transgress the boundary of the family as extended by Beccari. But in 1915 the Belgian botanist Hauman suggested a transgression. He had found a species from the Argentine to carry male flowers with no more than a single anther and, taking this as normal, named his species *Dioscorea monandra*; he suggested that it should have a section to itself—the Monandrae (*An. Mus. Naç. nat. Hist. Buenos Aires*, **27**, 336). Surely the condition is no more than an abnormality.

There are no genera in Dioscoreaceae not accounted for in the above section.

§2. *Dioscoreeae and para-Dioscoreeae: and the family boundary towards other Liliales*

In 1934 Hutchinson proposed (*Families Fl. Pl. Monocot.* p. 141) that: (i) the three genera *Trichopus*, *Avetra* and *Stenomeris* be withdrawn from the Dioscoreaceae; (ii) that the first two be upgraded with the family name Trichopodaceae; and (iii) that *Stenomeris* be upgraded with the family name Stenomeridaceae. Engler had experimented somewhat in that direction by making a tribe, Stenomerideae, of the three (*Vorlesungen Pflanzen-*

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[1] It is interesting to discover that a fruiting specimen of *Avetra* reached Roxburgh when he was in Calcutta, and was transmitted to Brown in London. No one could place it.

fam. p. 87, 1892). Neither suggestion is acceptable; not that they are untenable, but that they are too unphilosophical for a subject that is phylogenetic; Hutchinson's obscures the phylogeny and Engler's implies that *Trichopus* and *Stenomeris* are nearer to each other than their characters suggest. But it is convenient to have a non-committal name for the three, and they will be indicated in the following pages as the para-Dioscoreeae. The reader will find that the following key will help to clear up the position put before him:

Plants with hermaphrodite flowers—the para-Dioscoreeae.	
Ovules very numerous in each of the three loculi (Stenomerideae).	**1.** *Stenomeris*
Ovules 2 in each of the 3 loculi (Trichopodeae).	
Climber with a samara; 5 of the 6 ovules in the ovary aborting.	**2.** *Avetra*
Lowly herb, with a fleshy fruit which liberates its seeds by tearing.	**3.** *Trichopus*
Plants dioecious; ovules 2 in each loculus—the Dioscoreeae.	
Fruit a capsule	**4.** *Dioscorea*
Fruit a samara, 5 of the 6 ovules aborting.	**5.** *Rajania*
Fruit a berry.	**6.** *Tamus*

The Australian genus *Petermannia* does not belong to the family. Its only species, *P. cirrhosa*, climbs by tendrils; and it has numerous ovules on parietal placentas, but Ferdinand von Mueller, who was the first to describe it, assigned it to the Dioscoreaceae. Bentham, writing up the family for his and Sir Joseph Hooker's *Genera Plantarum*, though he did not proceed so far as to remove it, suggested that its proper place seemed to be in the Liliaceae; Hooker, writing up the Liliaceae, passed it by without mention: Bentham was certainly right.

It has been remarked, as for instance by Pfeffer, that twiners and tendril-climbers differ widely in that the former begin their search for light at the base of the upright woody plants which they victimize, whereas the tendril-climbers scramble up the better illuminated outside of the thickets which they use. It is unthinkable that a genus after having commenced to assert itself by twining would transfer the struggle to the other way, or that the reverse could occur. And *Petermannia* cannot have a place in the Dioscoreaceae. Twining is the criterion, not climbing. But plants unable to twine may yet be in the family if the cause of their inability be inadequate growth. There are indeed many of them. Of the alternative ways of accounting for their appearance in it—the one that they are relicts from the time when the proto-Dioscoreaceae were trying out the device of twining, the other that they are recessives that have fallen out of the competition with the woody Angiosperms—the latter is the right one. Later in this paper attention will be drawn to characters in stem and leaf evolved to aid in the efficacy of the twining effort, characters such as economically slender stems, long petioles, auriculate laminae and glandular leaf-tips; their presence even when actual twining is not developed declares the twining ancestry. Twining, as explained (p. 341), is a special addition to simple circumnutation. But circumnutation is not declared until the stems have length enough; and if they have not length enough, twining cannot be reached. The non-twiners in the Dioscoreaceae are dwarfed species.

'Stem twining' is not an exact statement of a character of the family, but 'stem twining whenever there is an adequate length of stem' is exact.

There is one dwarf in the para-Dioscoreeae, *Trichopus zeylanicus*; there are many dwarfs in the Dioscoreeae, even to the extent of composing whole sections in a degree which suggests that evolution of a dwarf has been easy. It has clearly rested in Dioscoreeae on a climate stable enough to establish them; for many of them are American and none of them are in Asia. *Trichopus* is at the same time a dwarf, a recessive and a relict—a recessive in that it must have come from a twining ancestry and a relict in that time has swept away all of its closer relations, leaving only *Avetra*, which indeed is not of the very closest affinity.

Trichopus and the dwarfed Dioscoreeae, however, have not fought an identical battle: the first adapted its economy to the enduring of shade; the others to getting along without shelter, for *Trichopus* grows on the floor of forest too overpowering for smaller shrubs to make a carpet of real service to a twiner, whereas the majority of the other dwarfs accept the shade of rocks for the shade of woody plants. The southern Andes harbour many lowly Dioscoreas and there are some as far north as Mexico. Again the Spanish Pyrenees harbour, chiefly in screes, the well-known *Dioscorea pyrenaica*, and in crevices its subspecies, *D. chouardii*. The South African *D. elephantipes* is a giant in comparison to these, but dwarfed in the assimilatory parts which surmount its huge tuber lying as a rule between protecting rocks. As far as one knows the rocky habitat is actually connected with humidity at the time of the renewal of growth.

A third habitat, occupied more sparingly than the rocky habitat, is an extension out of scrub into grassy savannah, and the number of species which have overcome the difficulties of acclimatizing themselves to it is small. The most interesting of them is the Madagascan *Dioscorea hexagona*. It shows itself dwarfed by the dryness of its position, by losing height in dry soil *pari passu* with the grasses, and becomes then strictly upright; but should its position be by a bush, which conserves the dew and is in itself a mark of a pocket of better conditions, its stem tips twine. This species has laminae that are rarely auriculate, and has short petioles; it has moved a considerable way from the typical *Dioscorea* though not far from some allies which occur in Madagascar.

One further remark regarding the rocky habitat is desirable; it is that *Tamus communis* invades rocky heath in the Mediterranean and may occur in the moister parts of Britain on not too abrupt sea-cliffs where sometimes shrubs and sometimes rocks provide broken shelter.

There is also a need to call attention to the stiffness of the branches produced in the South American section Sphaerantha which give the impression that they have a tendency to abandon twining. The section should be studied not only in its homeland where its relations to other plants may be clarified, but in cultivation where its twining may be measured.

The contention embodied in the last few paragraphs is that twining if not exposed is twining suppressed.

An analogy is useful here. A heap of gravel dropped on the shore before an incoming tide is dispersed and the material is removed according to the ease of moving it: if the heap be heterogeneous the effect is heterogeneous. So among the proto-Liliales: they were heterogeneous with some species tolerant of shade, others intolerant; and they were consequently with the part most tolerant of shade marginally competing vegetation. The tide of events and particularly the development of twining would intensify the shade-tolerance of their youth for the sake of illumination in later months, the annual habit being so binding that it could not be broken. On that happening the proto-Dioscoreaceae came into existence. We are not entitled to overlook the occurrence of a little twining outside the limits of Dioscoreaceae, as some species of *Asparagus* (Liliaceae-Asparagoideae), *Bowiea* (Liliaceae-Asphodeloideae), and *Herreria* (Liliaceae-Herrerioideae) and also *Stemona* (Stemonaceae) twine: they point to a tendency antedating the origin of the Dioscoreaceae; but that is all. Climbing by other means is more common, as in *Bomarea* (Amaryllidaceae), *Gloriosa* and its allies (Liliaceae-Melanthoideae) and *Smilax* with *Heterosmilax* (Liliaceae-Smilacoideae); and we may add *Petermannia*. So it is that if one of the Liliales should climb, it is outstanding if twining be adopted.

As already said, twining implies a size small enough for the twiner to start right under the victimized support.

Having started twining, natural selection acted in two ways. There was the yearly effort to make good against a growing support and the general effort to get new positions. It is not surprising if there should be along the line the appearing of recessive dwarfs.

It is worth noticing that dwarfing occurs in the Stemonaceae in a way reminiscent of the dwarfing in Dioscoreaceae and to remember how closely allied are the two families. Amaryllidaceae, as already said, is by no means as nearly allied; and the statement that it is the nearest should be forgotten; and so also should be the misleading simplification that has appeared in text-books that the Dioscoreas are *Smilax* with an inferior ovary. But a fact to be remembered is that the Asparagoid Liliaceae, which it is claimed are the nearest, are characterized by fleshy fruits and that the appearance of fleshy fruits in Dioscoreaceae is unusual. There are no more genera than *Trichopus* and *Tamus* in which they are truly fleshy (but see p. 398 for delay in drying). The fleshiness is not demonstrably for bird-dispersal: flood-water scatters the fruits of *Trichopus* and the juice of the berries of *Tamus* is irritant in the mouth, and though seeds are swallowed at times by birds, this is so seldom that it is not bird-distributed. It is the wind that is the usual agent; the seeds are winged, or in *Avetra* and *Rajania* the fruit is a winged samara. Considerable gain in length of stem must have come before the family became so dependent on the wind; but it might have left the rest of the proto-Liliales well before this dependence developed, as the only position for profitable wind-dispersal is from a distance above the soil; and as the stems are annual, fruiting had to be late and come when the vines withered.

The purpose of the matter under the next two headings is to show how para-Dioscoreeae and Dioscoreeae differ in ability to store food and to question how far they are apart in sex-differentiation.

§3. *The para-Dioscoreeae have less tissue for storage than the Dioscoreeae*

The underground storage organ of *Stenomeris* is an elongated swollen stem, rich in stored starch: unfortunately it is not yet adequately known, though that of *S. borneensis* was figured in *Gard. Bull., Straits Settlements*, **3**, 289, 1924, (the plants perhaps were immature). It appears as if it might be a whole branch and so homologous with a bulbil; but *Stenomeris* is not known to have aerial bulbils. A single stem arose laterally from each tuber figured, and sometimes the tuber branched. The largest tuber obtained was 8 cm. long. It is not exactly like any reproductive body in other Liliales.

The storage organ of *Trichopus* is unlike that of *Stenomeris*, for it is a typical but small rhizome, not much thicker than a pencil, horizontal with perhaps a slightly upturned tip, sparingly branched and closely covered by foliar scales. Aerial stems ascend from it. E. V. Watson described its cellular anatomy (*Notes Roy. Bot. Gard. Edinb.* **19**, 148, 1935).

Avetra is described as having a very short rhizome which is not tuberized. The writer has not seen it; but greatly hopes that the need of figuring it will be met.

There are no records for weight, water-content and food-content of the storage organs of any of these three; but they are all small. In contrast there is not a little literature on the tubers of the Dioscoreeae. Sir W. Hooker (*Guide to the Glasgow Botanic Garden*, p. 32, 1849) refers to a tuber of *Dioscorea elephantipes* weighing 700 lb. (365 kg.). This enormous weight could be only in part of living tissue; and though the weight of the tubers in this species is beyond overlooking, annual increment, ultimate maximum and many other valuable details remain quite unknown. Prof. Miège has recently stated (*Bull. Inst. franç. Afr. noir*, **20**, 45, 1958) that the root-stock of his *D. mangenotiana* may attain 60 kg.; but here again there is an unrecorded admixture of woody corm and parenchymatous lobes. The largest weight for the tuber of the cultivated *D. alata* is recorded as 62 kg.; and of this nearly the whole must have been food-storing tissue and the growth of a single year. The average marketable tuber of *D. alata* is less than 4 kg. and the average weight of the tubers of other species again less, but still very much more than the return from any of the para-Dioscoreeae. *D. sansibarensis* is recorded as reaching 30 kg.

The amount of water in the tuber of *D. alata* is about 70 % and it is evident that a tuber such as is commonly marketed holds a pint or more of it. It seems to me probable that the greater extension of the Dioscoreeae in the world over the para-Dioscoreeae is to be attributed to their water-store, as the latter must have rain at more frequent intervals than the former. The habitats of the para-Dioscoreeae are emphatic in regard to this. *Avetra* grows along the sandy east coast of Madagascar within a short distance of the sea where all the months of the year are rainy. *Trichopus* grows with freedom in Ceylon between the port of Galle and the mountain of Adam's peak where the deluges of the south-west monsoon are very heavy and again above the southern tip of India where rains are heavy; yet again in the Malay state of Kelantan on the inner edge of the sandy plain soaked through the north-eastern monsoon. *Stenomeris* grows in the same latitude of the Malay Penisula but on the other coast, then again in Borneo and eastwards to the wettest part of the Philippine archipelago. Field collectors have not been helpful in their notes; but one refers to sandy soil. It is proved of these para-Dioscoreeae that while needing the water, they must have open soil to back up their own water-pores in the removal of the excess. As to the amount of the rain, the annual fall at Tamatave in Madagascar, where *Avetra* grows, is 115 inches a year, and there is no rainless month; the rainfall behind Galle in Ceylon and at the south of India commonly exceeds 100 inches; and the fall is close on 100 inches where *Stenomeris* has been collected in Malaya. Tropical temperatures in all these places accompany the rain and there are two rain-peaks within the year.

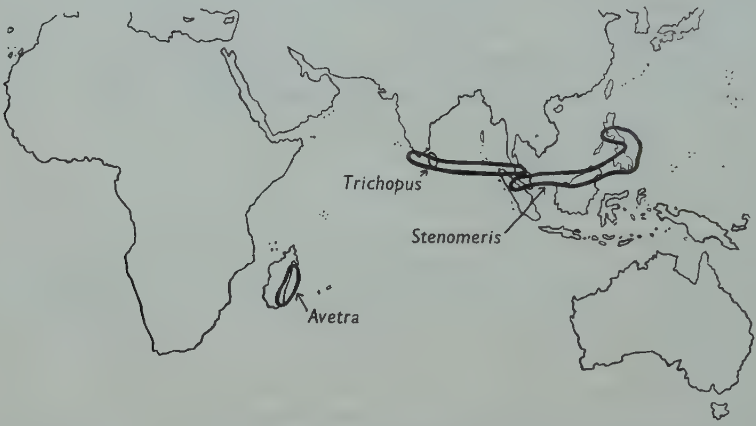

Fig. 1. The distribution in the World of the three genera of the para-Dioscoreeae.

The map above shows the localities to lie in an arc which may be called the 'Nepenthes Arc' because on it *Nepenthes* is at its intensest. Within the Arc, towards the east, the drought of Australia dries the climate; north of the Arc lower temperatures and drier conditions prevail and so the wet Arc is narrowed. Along it is the home of the Lemur monkeys which are tied by their food to rain forests, tied much as are the para-Dioscoreeae.

Avetra produces its flowers when the local climate is relatively dry, then ripens its fruits during the wettest months. These are stormy months and Perrier de la Bâthie describes the fruit as liable to be ripped off the vines by violent winds and to rot on the wet soil, and if not ripped off, the saturated air enables it to germinate in suspension. It is obvious that its samara will require more carrying power in the wind than the lighter seeds of the Dioscoreeae do, but not be carried far. The berries of *Trichopus* are ripped from the plants that bear them by flood-waters; they are produced where winds do not reach them. The flowers of *Stenomeris* have been collected in the Philippine islands in every month of the year except January, the want of records for January probably meaning no more than that it is then too wet for collecting. Presumedly its abundant winged seeds have no particular season. The flowers of all three genera nod and the pollen is thereby protected.

Macdougal has called attention to the use of the stored water for commencing growth (*Ann. Bot.* **26**, 71, 1912).

§4. *The whole of the Dioscoreaceae seek cross-pollination; and for the Dioscoreeae there can be no other form of pollination*

The Dioscoreeae, because the sexes are in different plants, need an agent to pollinate them; the para-Dioscoreeae have flowers manifestly constructed for pollination by insects and have devices intended to secure this in the form of cross-pollination. Attention may be drawn first to *Stenomeris* (see Fig. 2). As has already been mentioned, the torus is expanded into an urn and is suspended upside down, for the flower nods. Looking into the urn, the six stamens are seen with their broadened filaments inserted just within the rim; thence they are bent back towards the base of the urn and from the top of the filament the connective is prolonged as a bridge long enough to touch the stigmas and may be held in their stickiness. The pollination should be done by an insect which has already picked up pollen in another flower and now ascends one of the bridges seeking food and passes over the stigmas at the end of its upward journey; after searching for food the insect is much more likely to descend the wall of the urn than go by the way of entering and in descending to pass under and between the well-separated anther-cells, getting a charge of pollen in doing so; this charge should be carried then to another flower. The urn is of a green colour and the perianth-lobes are yellow in *S. dioscoreifolia*, or red in *S. borneensis*; but they are narrow and make a ring of short yellow rays rather than causing the whole flower to be conspicuous; however the ring may be as much as 35 mm. across and commonly is more than 17 mm. As the perianth lobes gradually part from each other and ultimately become reflexed, the circle widens and then narrows during anthesis. The urn itself may be 5 mm. across at the mouth. The perianth doubtless directs visiting insects, but not in that precise way by which flowers of higher evolution enable bees to carry out their diligent routine.

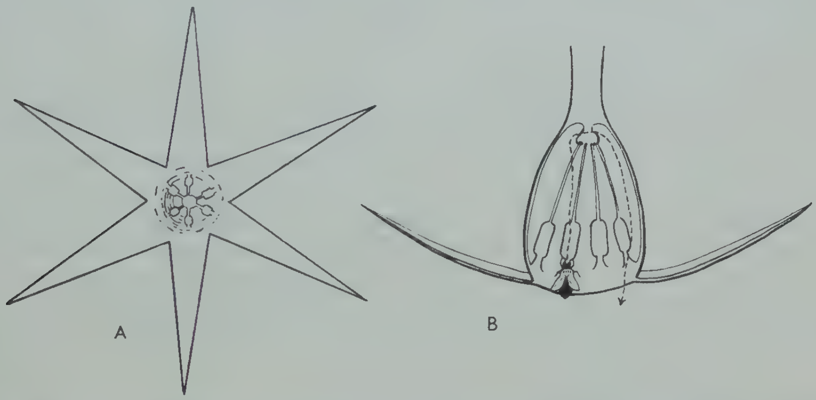

Fig. 2 A. The flower of *Stenomeris dioscoreifolia* as seen from below, i.e. looking into the urn and at the bridges which the extensions of the connective make to the stigmas, × 20. B. In vertical section showing the effective course of a visiting insect, × 30.

The flower of *Avetra* is white; and there is no urn, but a small pollination chamber. Perrier de la Bâthie says that insect visitors are numerous. He represents the flowers as directed downwards, their linear-lanceolate perianth lobes, which are up to 30 mm. long, making a narrowing passage up which the insects must crawl. Reaching the pollination chamber, they should enter it over the stigmas and leave it under the anthers, dropping out of the passage to go to another flower.

Trichopus has the mechanism of *Avetra* without the passage approach. Its flowers are smaller (see *Bot. Mag.*, plate 7350), of a dull purple passing towards the base to green. The slightly spreading perianth lobes give to the whole a width of 15 mm. The track that invites the insect to a way that cross-pollinates is supported by a flower-succession by which one flower only is open at a time; if it dies unfertilized, another is liberated to take its place by growing rapidly from between the scale-bracts of the *Bromus*-like spike. This succession goes on until there is fertilization. And, as is clear, the flower is intended to be crossed by insect agency.

Turning from the para-Dioscoreeae to the Dioscoreeae there is need to record first a great reduction in size. Recalling the postulate that the Dioscoreeae evolved after the para-Dioscoreeae the lesser size is particularly interesting: it appears as if the withdrawal of one sex had carried away half of the energy that should have gone into the building up of the flower. The usual diameter of the flowers is between 2 and 5 mm.; and only a few are considerably larger. Something must be said of them, and there is one statement to challenge. Uline stated (*Bot. Jb.* **25**, 147, 1898) that he had met with a plant—his *Dioscorea macrantha*—having a male flower up to $2\frac{1}{2}$ cm. across. Dr Knuth, when later he described it, increased this diameter to $2\frac{3}{4}$ cm. (*Notizbl. bot. Gart. Berl.* **7**, 198, 1917). It is astonishing in being far beyond anything that has hitherto been reported. The following records more usual occurrences.

Hauman assigns the diameter 9 mm. to the flower of *D. megalantha* (*An. Mus. naç. B. Aires*, **27**, 171, 1916); and this is large for a *Dioscorea* as the name implies. The African *D. buchanani*, which is the largest known of Africa, opens to 5–7 mm. at the mouth of the bell; press it flat as in a herbarium and it may measure even 11 mm. from tip to tip; but that is not its real diameter. In the other direction several species have flowers less than 2 mm. across, yet they are certainly entomophilous. Hauman correctly reasoned this from the character of the flower when (p. 446) he used the name *D. entomophila*; and he suggested flies as visitors, but he does not appear to have observed any. Nor indeed has anyone else. It was absurd to attribute, as has been done, fertilization to the wind, for the pollen is glutinous. Reiche's suggestion (in *Bot. Jb.* **42**, 186) that pollen falls from the male on to the female flowers does not seem reasonable even if this be aided by the splash of heavy drops of water from above. In Britain and in Switzerland, and doubtless elsewhere, pollination of *Tamus communis* results from the visits of flying insects (see *Proc. Linn. Soc. Lond.* **157**, 99, 1944); they are in large part tissue-puncturing insects as contrasted with nectary-licking insects. The flowers of *Tamus* when open are 3–4 mm. across.

A reasonable supposition is that pollination of many species in the tropics is done by night-flying insects, so that guidance by vision is not asked for; often there is an attraction by scent, strengthened by the co-operation of a number being open together. This co-operation is exposed by the manner in which fertile capsules become grouped in the infructescences. Examine these infructescences: there is possibly a grouping of infertile flowers attributable to a soaking night; then a group of fertile capsules, the result of a good night; followed by another group of infertile flowers. The appearance of the female flowers in anthesis is not like that of the male flowers; the width may be a little greater; if visiting be directed by scent, the slight difference between the two sexes would not greatly matter.

In a few species of the Dioscoreeae the colour of the male flowers is other than green; in a dry state it may be a purple that is nearly black. If like *Stenomeris* that colour appears during drying, we need to know what the colour is in life. The deep-coloured flowers are chiefly on American species. The Old World *Dioscorea bulbifera* has male flowers reddish as autumn leaves. In some species of both the Old and the New World the flowers are without chlorophyll and nearly white. Often there is evidently no free honey. As we have fossil bees from the Cretaceous, there is nothing against the very early Dioscoreaceae being entomophilous.

A typical flower has six fertile stamens; a very common state is for them to be reduced to three by the sterilization (and sometimes absence) of the upper whorl. The loss affects the whole whorl equally. There is a species in China and others in the West Indies, Mexico and South America with only three fertile stamens, but the filament of the fertile stamens is bifurcated so that a ring of six points presenting pollen is restored. Sterilization of one whorl of stamens may be accompanied by their enlargement and conversion into obstacles to the free movement of visiting insects, compelling a rubbing against the dehiscing anthers of the fertile stamens. Services such as these proclaim beyond doubt insect pollination.

§5. *Imperfect sex separation in the Dioscoreeae*

The postulate that the sex separation which we see in the Dioscoreeae evolved from hermaphrodite flowered ancestors leads to a hope that somehow traces of the process may exist. But Nature must and does rapidly eliminate interferences with multiplication; and the hope is weak, but it behoves us to collect as much knowledge as we can.

To date we do not have a single proved case of the two sexes being fertile on the one individual: what we have is records of imperfect male organs and imperfect female organs intruded into what may be fertile individuals of the other sex. They are seen unevenly mixed, almost always more of the male on a female plant than of the female on a male. The intermediate has never been observed carrying in equal degree indications of both sexes. As the records are scattered, an attempt is made here to review them. Sex disturbance has been reported in the following: 1,[1] *D.* (*Opsophyton*) *bulbifera*; 2, *D.* (*Enantiophyllum*) *cayenensis* under the name *D. liebrechtsiana*; 3, *D.* (*Monadelpha*) *coronata*; 4, *D.* (*Enantiophyllum*) *japonica*; 5, *D.* (*Cycladenium*) *kuntzei*; 6, *D.* (*Monadelpha*) *lagoasanta*; 7, *D.* (*Cycladenium*) *lehmannii*; 8, *D.* (*Cycladenium*) *lundii*; 9, *D.* (*Cycladenium*) *megalantha*; 10, *D.* (*Polyneuron*) *minima*; 11, *D.* (*Monadelpha*) *monadelpha*; 12, *D.* (*Polyneuron*) *multinervis*; 13, *D.* (*Enantiophyllum*) *opposita* under the name *D. batatas*; 14, *D.* (*Monadelpha*) *praetervisa*; 15, *D.* (*Lynchnostemon*) *polygonoides*; 16, *D.* (*Brachystigma*) *sinuata*; 17, *D.* (*Stenophora*) *tokoro*.

Twelve of the seventeen are species from the New World. Four of them belong to the section Monadelpha and four to the section Cycladenium; two each to Enantiophyllum, Stenophora and Polyneuron. It thus appears as if the sexual separation is less incisive in the New World than in the Old and more likely to appear in some sections than in others. The abnormal species of the Old World are rather conspicuously those of cultivation but that may be because they particularly attract attention.

Hauman, in describing his *D. coronata* (*An. Mus. naç. B. Aires*, **27**, 480, 1916) claimed male inflorescences to occur on the lower part of the plant and female on the upper; he was later to get normal unisexed plants. De Wildeman claimed different sexes on different branches of a plant of *D. cayenensis* (*Diosc. aliment. et tox.* p. 196, 1938); but he was using collectors' dried specimens or notes; and collectors are not always to be relied on. Grisebach, when he described *D. megalantha* (*Symb. Fl. Argent.* p. 323, 1879), attributed to his type-plant—lowest flowering axes male and upper female. Hauman, who had discovered a specimen of Grisebach's naming in the possession of the University of Cordoba, found that this specimen had male and female flowers on its lowest inflorescences, adding (on p. 471) that the condition was rare, but only five lines lower that it was common. Knuth quotes the latter statement which is the less credible of the two. The distribution on *D. polygonoides*, *D. minima* and *D. multinervis* is said by Uline not to be in any order.

[1] For nos. 1 and 4 see Prain & Burkill in *Ann. Roy. Bot. Gard. Calcutta*, **14**, 116; for no. 7, 260; for 13, see Carrière in *Bull. Soc. d'Acclimat.* **1**, 373 and *J. Hort.* p. 111, 1855; for 17 see Süssenguth in *Beih. Bot. Zbl.* **38**/**2**, 43, 1921; and for most of the others see Uline in *Bot. Jb.* **25**, 147, and Knuth, at various pages in his *Dioscoreaceae*.

Within the town of Singapore, doubtless from former cultivation, a race of *D. bulbifera* recently grew, carrying when it flowered spikes with seemingly perfect male flowers above the base, but at the base imperfect female flowers. Plants behaving in exactly the same way exist in the Singapore herbarium from the Langkawi islands and from Java where they are called by a name meaning 'the Singapore tuber'. It is reasonable to think that the three represent one and the same clone and to believe it to have been passed from one place to the other two. If that be right it illustrates a sex-permanence in the clone. Should it be possible to recover the clone in the condition of bearing seeds, the sexual state of the seeds would be worth investigating. Süssenguth (*loc. cit.*) made the most use he could of finding both sexes in the flowers of *D. sinuata* and *D. tokoro*. The anthers of the outer three of the six stamens he found to have suffered arrest when the pollen had reached the tetrad stage and those of the inner three a trifle earlier. This is in accord with the fact that in all the species of *Dioscorea* that have the fertile anthers reduced to three it is the outer three that remain. It may also be added that *D. tokoro* has the three-stamened *D. gracillima* for a near ally. Undeniably the inner whorl of stamens through the Dioscoreas is not so secure of production as the outer, is indeed weak, and is lost in so many sections of the genus as to be a definitely inferior taxonomic character. Uline made too much of it when he used for cutting apart section after section the number of fertile stamens present.

Uline noticed the pedicel of the male flower to have a slightly greater diameter under the flower than lower down and suggested that the swelling represents the absent ovary; but it is better regarded as support for the perianth, i.e. is the torus.

§6. *Superfluous synonyms*

A century ago when the Dioscoreaceae were but superficially known and when in consequence species appeared to be more isolated from one another than they really are, the temptation to found genera led to the appearance of many names that require listing for the purpose of research, but not for more.

First, there are two based on actual errors of diagnosis—*Oncus* of Loureiro and *Botrysicyos* of Hochstetter. *Oncus* covers *Dioscorea esculenta*: *Botryosicyos* covers *D. quartiniana*. Delponte's *Sismondaea* is thought to be *D. piperifolia*, indifferently defined. As not being distinct enough for generic rank, are Miègeville's *Borderea* and R. A. Salisbury's *Testudinaria* and they are to be down-graded to sectional rank. Uline's *Higinbothamia* if not abandoned must be down-graded. Salisbury proposed as genera *Hamatris* being *D. pentaphylla*, *Merione* being *D. villosa*, *Polynome* covering *D. bulbifera* and part of *D. alata*; *Strophis* being *D. cirrhosa*; and *Elephantodon* being a clone of *D. alata*. To Salisbury such as *D. polygonoides* (*D. martinicensis*) alone belongs to *Dioscorea* Of his new names none but *Testudinaria* is wanted; the rest he left in a manuscript which Gray printed in 1856, or some 36 years after he had devised them.

One further name remains—Philippi's genus *Epipetrum*. Pavon had collected the plant in 1788 in Chile; and as it is by no means rare near Santiago, Bertero, Cuming and Bridges in their turns obtained it. It did not get a name under *Dioscorea* until Colla in 1836 called it *D. humilis* and Hooker in ignorance of Colla's name called it (1844) *D. pusilla*. In 1883 Philippi sought to separate it under the name *Epipetrum*. The characters he assembled do not justify his contention and this he himself further weakened by adding to *Epipetrum* in 1896 two new species that bridge the gap between it and other Dioscoreas. But in 1908 Karl Reiche announced (in *Bot. Jb.* **42**, 178) an underground structure for *E. humile* which, could one believe all he claimed, might establish *Epipetrum*, on new characters. Awaiting a fresh examination the proper place for *Epipetrum* is within *Dioscorea*.

Pax, when he united *Borderea* and *Epipetrum* into a single genus, showed that he had not discovered on what characters his taxonomy should have been built.

II. In search of the remote past

§7. *The geological record*

The testimony of the rocks is poor; it is not until the Eocene that undoubted impressions are found. Lesquerreux thought that he had one from the chalk of Dakota, United States, and called it *Dioscorea cretacea* (*Monogr. U.S. Geol. Surv.* **17**, 156, 1874); but his determination is not acceptable, though that there were Dioscoreaceae in the Cretaceous is demonstrable by other evidence and from another part of the World. The Atlantic Rift in the end of the Cretaceous parted the coasts now those of Brazil and the Argentine from the opposing coasts of Africa; and the present-day dispersal of *Dioscorea* demonstrates that the Rift cut into two the family as then represented in that part of the World, whereafter the halves evolved independently. One result is that no species or section of the genus is common to the two regions. Unco-ordinated evolution has changed the aspects so completely.

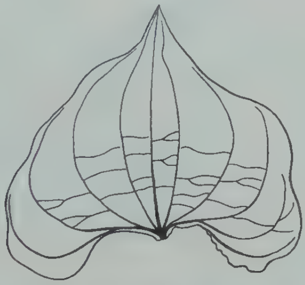

Fig. 3. The leaf of *Dioscorea lyelli* (*Dioscoroides lyelli* Fritel) from Potonié, *Lehrbuch d. Palaeobotanik*, p. 356, 1921.

If it had been possible the next part of this paper would be a comparison of Dioscoreas found today on either side of the Rift in an attempt to integrate all the sections into which they fall; but those of South America have been so superficially studied that this is not possible, and those of Africa could be better known. Knuth's monograph of the family, most useful for the immense amount of information in it, is not constructed so as to be helpful here.

In the mountains near Itatiaia, inland from Rio de Janeiro, grows an extremely interesting species, *D. perdicum*. It was described in 1892 (in *Bot. Jb.* **3**, Beibl. **23**, 13). It grows in short moorland grass and it has a rhizome which apparently is scarcely buried by soil but may be hidden by moss. A suggestion has come from the Botanic Garden at Rio that it and *D. plantaginifolia* are conspecific; if they are not conspecific but genuinely allied, we find at least two rhizomatous species in subtropical South America, and it is time to seek for more. Knuth with a query classified *D. perdicum* in the section Cycladenium and made a remote section, Pedicellatae, for *D. plantaginifolia*, (confusing with it a Menisperm). As *D. perdicum* most certainly does not belong to the section Cycladenium, the name Pedicellatae may be allowed to provide a sectional name for it. The important fact, however, is not its section, but the recognition that there is a rhizomatous section in South America.

It is not possible to advance anything against the theory that Dioscoreaceae when they parted themselves from the rest of the proto-Liliales were rhizomatous; therefore the section of *D. perdicum* and the Stenophoras of China, etc, share in their rhizomes a primitive character; and their geographic remoteness from each other suggests that rhizomatous Dioscoreas at one time had travelled through the intervening continent of Africa, and were enabled to maintain a place about the southern Atlantic from the close of the Cretaceous.

The presumable course of evolution from this 'proto' rhizome to the prevalent tuber of today is given on p. 346–47 below. Evolution contracted the rhizome into a tuber, the whole of which was perennial, as in the section Testudinaria and as in *Tamus*. On looking across the Atlantic we find a great number of species with tubers, the whole of which are perennial, and it is argued from this that, at the time of the Rifting of the Atlantic, evolution had proceeded so far in the *Testudinaria-Tamus* direction that South America

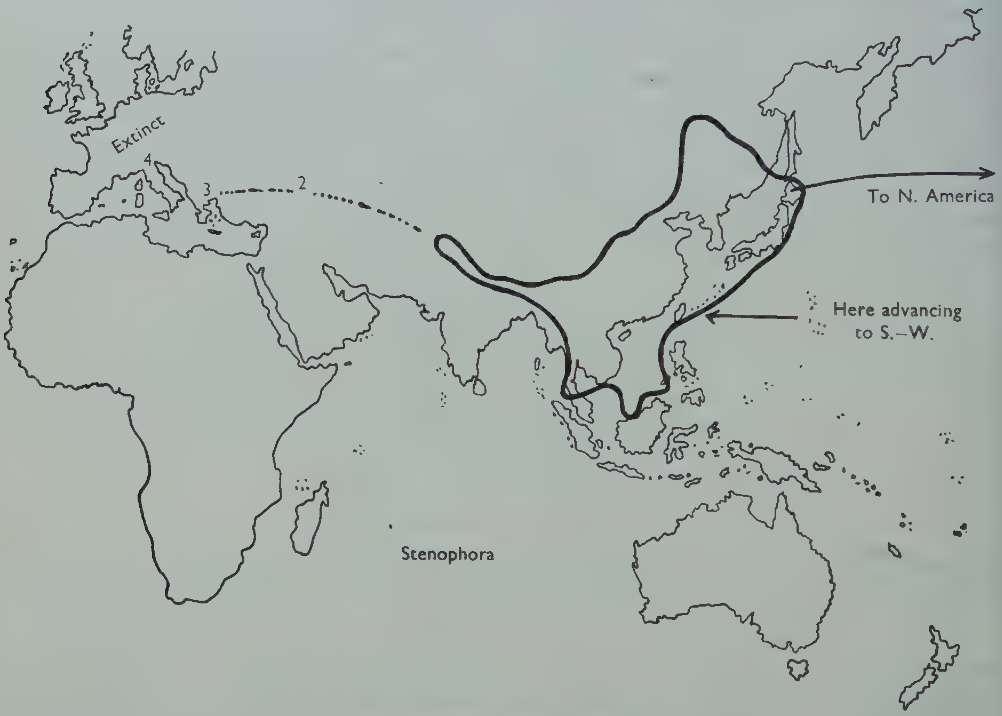

Fig. 4. The distribution of the section Stenophora in the World. 2 *D. caucasica*; 3 *D. balcanica* 4, Eocene fossils.

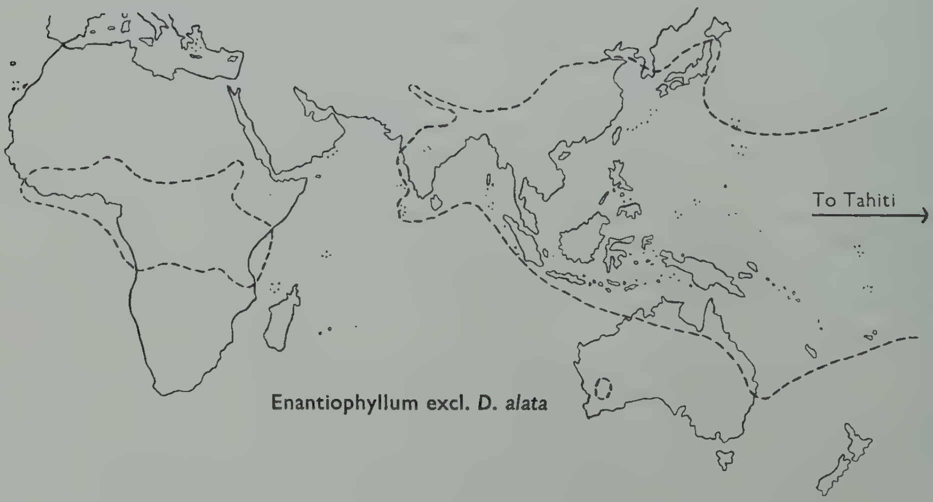

Fig. 5. The distribution of the section Enantiophyllum in the World excluding the cultigen *D. alata*

was freely stocked with tuberous species but with the rhizomatous condition still intermixed.

On the Old World side of the Rift the reduction of the rhizome was accompanied by the evolution of an annual lobing for storage—a lobing with which, on account of its generality, botanists have reason to be very familiar. This lobing is not as yet definitely proved for any American species. If it be proved, then lobing was being evolved when the Rift occurred.

I turn to another barrier made by water—the Tethys. This oceanic sound extended from that part of the Pacific which is now the China Sea to the Atlantic, and the other end is discernible even in the American coast-line; but we have here no concern with its dying out. During its history it varied in breadth from time to time; and it suffered interruption, followed by reopening and a final interruption as the Himalayas rose. The dispersal of Stenophora, set against the history of the Tethys, can thus be interpreted: a small part of *Dioscorea* was enabled to obtain a place to the north of the Tethys where it evolved in isolation without the alteration of its inherited rhizome into a tuber; it throve well enough to extend from China to Europe (see map, fig. 4) in the Eocene, at which time the final blocking in Asia of the Tethys liberated it to acclimatize itself southwards in an advance into the Indian monsoon rains whereby its front has since moved forward to a line from the eastern end of the Himalayas through Burma to the edges of Malaysia. If the reader will turn to my account of the Dioscoreaceae in the *Flora Malesiana* (**1**/4, 304, 1951) he will find the vanguard indicated, and again indicated in Fig. 4 (p. 330). Fig. 3 (p. 329) is from an Eocene fossil and shows the marginal sinuations enabling it to be assigned to the section Stenophora.

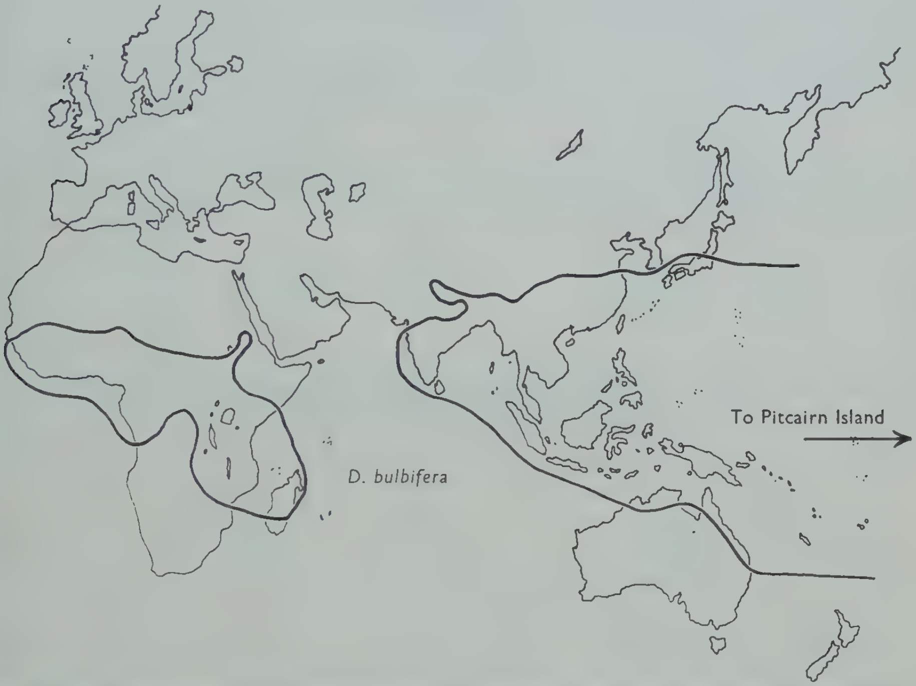

Fig. 6. The distribution of the only species—*D. bulbifera*—that extends over two continents, showing its interruption between Asia and Africa.

The blocking of the Tethys, when it liberated the Stenophoras for their advance southward, liberated the Enantiophylla to interdigitate with them, by advancing northward. During the mild Miocene—so mild that a suggestion has been made that ice may have disappeared entirely from the World—the Behring Straits became blocked and, when cold water was excluded by this from the northern Pacific, the bridge that shut it out served for the passing of elephants and rhinoceroses into America and horses into Asia. With the elephants went many forest trees (see, for instance, Gray in *Mem. Amer. Acad.* (N.S.) **6**, 1858 and Hooker in *Ann. Nat. Sci.* (**6**) *Bot.* **6**, 326, 1878), and with the trees

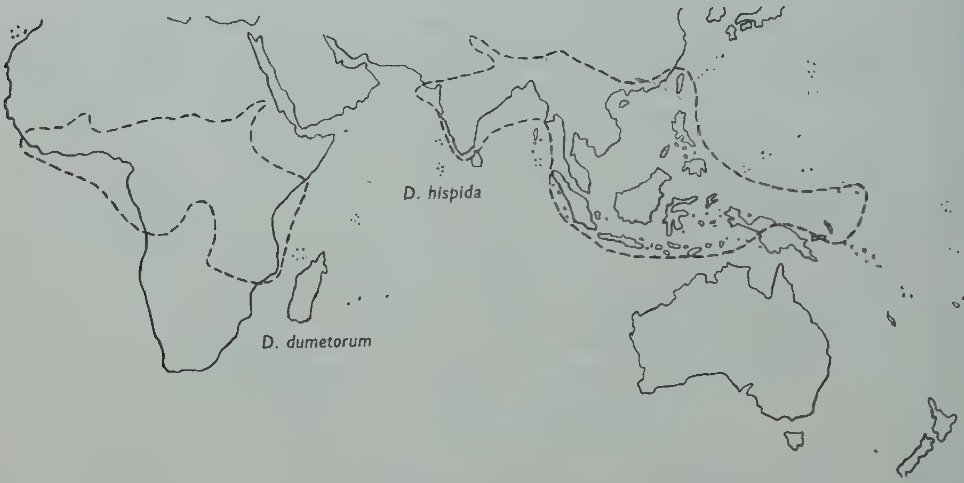

Fig. 7. The distribution of *D. dumetorum* and its close ally *D. hispida*; and the break between Asia and Africa which presumedly favoured their separation.

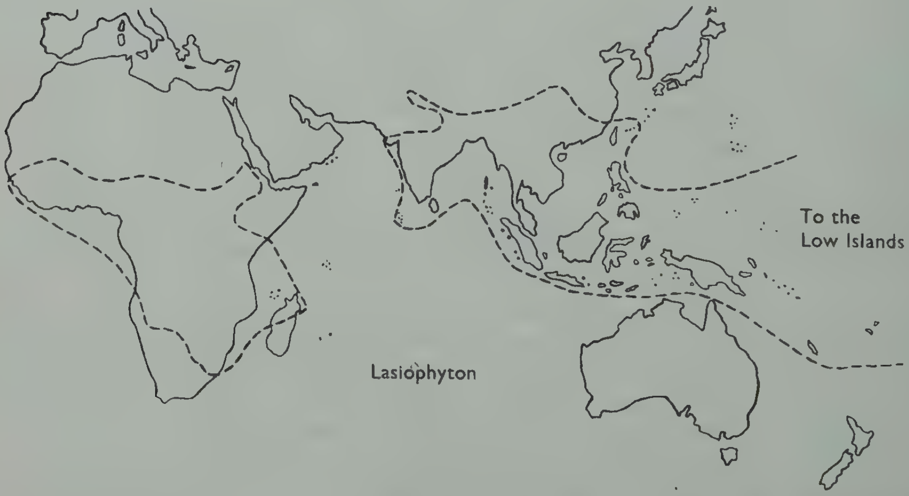

Fig. 8. The distribution of the section Lasiophyton showing the width of the break between Asia and Africa that interrupts its continuum.

certain forest herbs. Among them went a representative of the section Stenophora. It would seem that the section Enantiophyllum had not as yet acclimatized itself so far north as to get on to the bridge. When the bridge had gone, the inflow of cold water being renewed, the climate drove whatever of Stenophora there was altogether from the northwestern side of North America, leaving it in eastern Canada and the eastern United States. The reader, by comparing the maps, Figs. 4 and 5, will observe that today

Stenophora extends northward—we may say still extends northward—farther than Enantiophyllum.

There is reason to think that the Tethys, which at one time sprawled over the area of the Sahara, always limited the Stenophoras to Eurasia; and in Europe in the Eocene they would be subjected to considerable heat as the Equator was then to their immediate south. The retreating Equator might have had more to do with their loss of place in Europe than the subsequent Ice Age, as in the matter of time it was much nearer. *D. balcanica* and *D. caucasica* would be relicts in Europe of Eocene *Dioscorea* rather than recoveries of position after the Ice Ages by migration along the Himalaya.

The next barrier grew up as the Miocene passed away. An adequate humidity accompanying a high temperature had allowed the Dioscoreaceae to maintain a continuity between the Dioscoreas of Asia and Africa over land connecting the continents: but in time the humidity failed and the climatic continuum was broken; and the time-gap from then to now has been enough to lead to all the taxa concerned diverging at specific level, except *D. bulbifera* which is in course of diverging at varietal level. These three sections straddle the gap now.

In the maps (Figs. 6–8) are given the present-day dispersals of *D. bulbifera*, of the whole of the section Lasiophyton and of the section Enantiophyllum (excluding its pantropic cultivated *D. alata*).

The reader, on comparing them, will observe in each map that the westward extension of the eastern half ends at the same position—71° E.—and that the line turns northeastwards similarly. This has enabled an estimate to be made of the amount of rain that the Dioscoreas require over their six months of most vigorous growth: it has been found to be roughly 30 inches (see *Ann. Roy. Bot. Gard. Calcutta*, **14**, 433, 434 and 486).[1] Thus we understand how as the good humidity of the Miocene began to give way a pocket of inadequate humidity appeared and spread. Today it is as wide at the Atlantic, and as effective as the Atlantic, it would seem, in isolating lines of evolution but coming so much later one species, *D. bulbifera*, has been left on either side of it.

As India is found to be drying, the gap cannot be lessening. Its sharp limits in India are intriguing; will the limits on the African side be as suggestive?

We have in the occurrence of the three sections on either side of the gap evidence of their former existence in the gap and it proves the existence of the sections before the break became effective. We have seen that the Atlantic Rift came before any of the extant sections took shape; we have uncovered something regarding the section Stenophora in the history of the Tethys and light on the sections Opsophyton, Lasiophyton and Enantiophyllum from the history of the barren Middle East. There is yet another glimmer: it relates to the section Borderea. There was no Sahara when the Pliocene gave place to the Pleistocene, but intersecting waterways, and it would seem opportunities existed for the Dioscoreaceae such as could enable Borderea to occupy positions from the Atlantic to Abyssinia, so we find the section now represented by *D. pyrenaica* high in the Spanish Pyrenees, by its subspecies *D. chouardii* lower down in the gorges, by *D. gillettii* to the south of Abyssinia in Kenya: and at one time it obviously had intermediate stations of which we have no visual evidence.

The reader must be told here, in anticipation of a later reference, that the genus *Tamus* is phytogeographically of the same group as Borderea. It survived the drying of the Sahara, as *D. pyrenaica* did, on the moisture of the Atlantic margin of the land. Borderea under the threat became dwarfed and then all but went out of existence, while the three sections Opsophyton, Lasiophyton and Enantiophyllum lost by the desiccation so small a part of their area that they have had a vigorous existence both east and west of the gap. There is no evidence for the climatic continuum of the Miocene having enabled one continent to supply to the other Opsophyton or Enantiophyllum, the other being previously without it. The association with high forest of Enantiophyllum is the same in both continents as if it had been a character of the section older than the development of the gap. Its underground parts in Africa are developed in a way which seems to demand time; and its gain of dispersal in Asia, equally demanding time for the acclimatization by which it entered China and reached Western Australia. This looks like the possession of a wide dispersal before the Miocene. However, turning to Lasiophyton, the dispersal of the two species *D. dumetorum* and *D. hispida* is such as to suggest that Asia received the ancestry of *D. hispida* from Africa and, if so, possibly through migration in the Miocene continuum. The reason for suspecting *D. hispida* of delayed arrival in Asia is its absence from Ceylon and the Andaman Islands, and indications that Man has been taking it farther towards the East than its own power of spreading. But no other Asiatic species of its section show delayed arrival.

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[1] Since 1938 when this volume was published, all the Dioscoreas concerned have been proved by Santapau and Raizada to occur in the Gir forests—a slight extension westwards, but so slight as not to alter the findings.

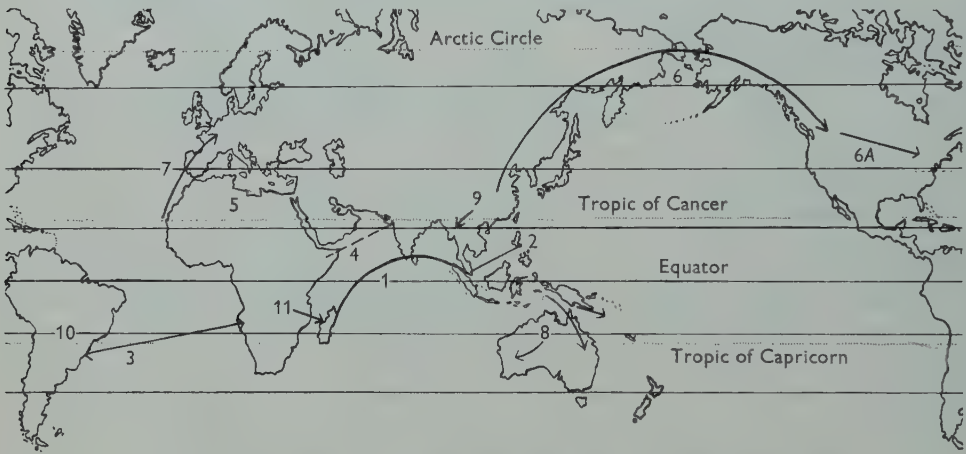

Fig. 9. Migration lines and positions of importance in the history of the Dioscoreaceae: 1, the part of the *Nepenthes* Arc occupied by *Avetra* and *Trichopus*; 2, its continuation occupied by *Stenomeris*; 3, where the rifting of the Atlantic broke continuity; 4, the severance due to the Pliocene drought following the Miocene continuum; 5, where Borderea may have been obliterated; 6, the section Stenophora crosses to North America; and 6 *A* survives by crossing the continent; 7, *Tamus* follows the beech (*Fagus*) northwards after the Glacial Period; 8, Enantiophyllum advances southward and eastward; 9, Stenophora advances southwards; 10, the only known part of the New World where a rhizomatous species is reported; 11, the route into Madagascar for the line that gave the greater part of its endemic species.

Before closing this geological summary, a few words need to be said on the variable rate of evolution, lest we find ourselves asking for the same rate without proving the same conditions.

It is right to claim that evolution is hastened or delayed by circumstances. A period of cataclysms is a time of destruction when the weaker species are eliminated; a calm period in succession favours the spreading of the strong; a repeated alternation between weeding out and encouragement to spread leads to so-called explosive evolution in species attuned to the alternation. The Earth has had such periods; but what is true of time is true of space.

The continent richest in species of *Dioscorea* is South America. And that circumstance is attributable to it having had in the later Tertiary the greatest area both in its lowlands and its mountains of steady humid climates particularly suitable for speciation. Expect therefore the species to be badly characterized.

Knuth's statement that Africa is the continent richest in species appears incorrect.

§8. *The immediate antecedents of the Dioscoreaceae*

On p. 320 a first impression of the nature of the proto-Dioscoreaceae was given: here follows an attempt to reason how they emerged from the trunk lines of the proto-Liliales by the use of the only possible evidence, namely by comparing the living Dioscoreaceae and living genera from other families of the Liliales. I desire to show that a single line was likely. It is scarcely necessary to draw into the argument Juncaceae, Haemodoraceae, Iridaceae and Velloziaceae, as it is easy to see that they were not involved in the emergence: Amaryllidaceae, Stemonaceae, Taccaceae and in particular the Liliaceae remain in view.

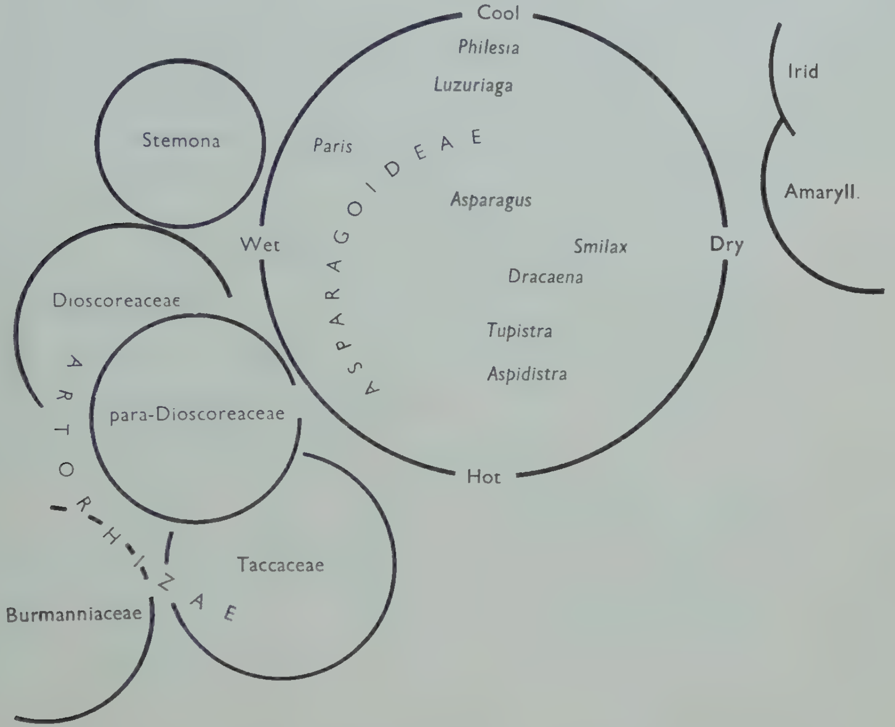

Fig. 10. A diagram suggesting how the families closest to the Dioscoreaceae came out of the proto-Liliales. Discussion in the text.

Liliaceae present phylogenetic difficulties. While fairly homogeneous in flower, they are so heterogeneous in vegetative parts that taxonomists have been tempted to advocate subdivision, raising all these to family level—Smilacaceae, Philesiaceae, Agavaceae, Trilliaceae, Hypoxidaceae, and Ruscaceae. Sir Joseph Hooker, in his *Genera Plantarum*, and Prof. Adolf Engler more recently, have alike resisted such division, and are followed here. Engler's system provides as subfamilies—Melanthoideae, Herrerioideae, Asphodeloideae, Allioideae, Lilioideae, Dracaenoideae, Asparagoideae, Ophiopogonoideae, Aletroideae, Luzuriagoideae and Smilacoideae and such as are wanted are used here. A tri-dimensional family tree of the Liliales would have Liliaceae rising like a tree-trunk centrally, the families such as Dioscoreaceae taking origin from it like stolons and the subfamilies at higher levels like branches, stolons being derivatives of long standing, branches newer in time. The idea is incorporated into the diagram (Fig. 10) which has been prepared to illustrate the deductions which now follow. Its large central circle represents the family Liliaceae: the smaller circles about it represent lesser families that have come out of the proto-Liliales; the proto-Liliales are to be imagined as in support. The big circle has been quartered—a quarter for coolness opposed to a quarter for heat, and a quarter for dryness opposed to a quarter for humidity. The wide distribution of the living Liliales makes it reasonable to assume that no one of these four climatic conditions was forbidding to the proto-Liliales. The derived families emerged under the influence of one or another; and their circles are placed appropriately about the central circle. Within the big circle are the names of a few taxa belonging to the Liliaceae, their positions being relative to the positions of the smaller circles with the purpose of suggesting alliance to the smaller families. The reader will observe the subfamily Asparagoideae in position close to the Dioscoreaceae, and that on the same side of the large circle are the Taccaceae and Stemonaceae; but that the Iridaceae and Amaryllidaceae are in the opposite quarter. It has been written (Solms-Laubach in *Bot. Ztg*, **36**, 66; Uline in *Bot. J.* **25**, 163 and Knuth in his *Dioscoreaceae*, p. 35) that the Dioscoreaceae stand nearest to the Amaryllidaceae. With this statement I disagree: phylogenetically it could not have been so. Taccaceae and Stemonaceae are nearer. The progress of evolution has obliterated the stages by which all three emerged from the proto-Liliales; but more so those of the Dioscoreaceae, as if its entry into competition with woody plants by the use of twining for support needed prompt adjustment to reach success. Of the three the Taccaceae enlarged its leaves; the other two extended their stems. If the area over which they are now distributed can be used for measuring their success, the Taccaceae have been much less successful than the Dioscoreaceae.

On the other side of the large circle are the families which expose ground rosettes to the full sun and, needing no petioles for gaining light, not uncommonly sink the lower end of the assimilating leaf into the soil in the protection of a coated bulb. On that side of the large circle the season of growth could allow time neither for spreading large leaves nor extending stems. Obviously the Dioscoreaceae and the Amaryllidaceae did not evolve in close association. The subfamily suited for the place within the large circle inside Amaryllidaceae is the Allioideae.

Following up the remark made on p. 322 that *Dioscorea* is not *Smilax* with an inferior ovary, a little clarification on the use of Smilaceae, Smilacaceae and Smilacoideae as subdivisions of Liliaceae is in place here. In 1789 de Jussieu gathered under the name 'Asparagi' (*a*) *Dioscorea*, *Rajania*, *Tamus*, (*b*) *Dracaena*, *Dianella*, *Polygonatum*, *Callixene* (i.e. *Luzuriaga*), *Philesia*, *Medeola*, *Trillium*, *Paris*, *Convallaria*, *Ruscus*, *Smilax*, and (*c*) *Flagellaria*. The first three are of Dioscoreaceae, the rest, except *Flagellaria*, are of Liliaceae. He repeated the list in 1791. Ventenat, in 1799, separated the three Dioscoreaceae and, adding *Smilax* and *Ruscus* to them, called the five Smilaceae; the rest he called Asparagoideae (*Tabl. Regne végétal*, **2**, 146). Ventenat's name may be called Smilacaceae no. 1 to avoid confusion as four different groups followed each with *Smilax* as a name-genus. Ventenat called the rest Asparagoideae. Augustin Pyrame de Candolle was engaged at the time in producing a Flora of France by revising Lamarck's and he put these genera of the French flora together—*Tamus*, *Ruscus*, *Asparagus*, *Convallaria*, *Maianthemum*, *Streptopus*, *Paris* and *Smilax*, using the name Asparageae and commenting that they held together well. At any rate he had obtained a reasoned collection which Linnaeus's Sexual System had scattered over almost as many 'classes'. The nucleus of what was to come was in the work of these three French botanists. Then Brown, as already stated (p. 320), took *Tamus* away from the plants with berries, where De Candolle had had it, and uniting it with *Dioscorea* and *Rajania* made his Dioscoreae (*Prod. Fl. Nov. Holl.* p. 294), later to be better named Dioscoreaceae. These—*Smilax*, *Rhipogonum*, *Drymophila*, *Trillium*, *Paris*, *Medeola*, *Convallaria* and *Streptopus*—he called the Smilaceae (for Smilacaceae), not using the name as Ventenat had done. For the sake of clarity we may call Brown's Smilaceae Smilacaceae no. 2. Brown recognized a third group which he called Asphodeleae, its name genus *Asphodelus*. Lindley in 1835

(*Introd. Nat. Syst.* ed. 2, p. 359) regarded Brown's dividing line between Asparageae and Asphodeleae obscure and swept into Asparageae all his Asphodeleae except *Streptopus*, reducing at the same time the Smilaceae to no more than *Smilax* and *Rhipogonum*. Lindley's may be called Smilacaceae no. 3. He set up *Aspidistra* as Aspidistreae: earlier botanists had not placed it. Endlicher followed and created Smilacaceae no. 4 by transferring most of the Asparageae to Smilacaceae: and his treatment dominated the classifications used by succeeding French and English botanists up to the publishing of Bentham and Hooker's *Genera plantarum* (1883) wherein Smilacaceae was reduced to a tribe—Smilaceae no. 5—of the Liliaceae, and this was adopted by Engler (*Pflanzenfam.* **2/5**, 19, 1888) who, suggesting the name Smilacoideae as a subfamily and resorting to the name Asparagoideae, considerably clarified the taxonomy. Hutchinson has followed him in reducing the taxon which holds *Smilax* to the least possible size. In review Ventenat's taxon was this reasonable minimum together with the Dioscoreaceae; Brown's the minimum together with *Drymophila*, *Trillium*, etc. as above; Lindley's in 1835 the very minimum; Endlicher's at the other extreme; he greatly enlarged it and was followed by Kunth, Le Maout and others until 1883 when Bentham and Hooker (Hooker to be precise) reduced it again to its minimum; Engler in 1888 agreed and Hutchinson has agreed also. The concensus of opinion has thus shaped itself to great advantage.

Engler's Asparagoideae covers six or two-fifths of the genera that de Jussieu had under Asparagi.

Though in Fig. 10 the Asparagoideae face Dioscoreaceae across the boundary of the large circle, as climbers versus non-climbers, they differ also in that dry fruits characterize the Dioscoreaceae and fleshy the Asparagoideae—not quite completely, but nearly so. Could the adoption of the wind for seed-dispersal have been a sequel to the attaining of a length of stem adequate to bring the seeds into the wind, the growth of the stem, by delaying flowering, bringing the fruit-ripening to the end of the season? I think so.

It has been mentioned on p. 322 that there are twining species in *Asparagus* itself. Inversely, there are fleshy fruits in *Tamus* and *Trichopus*. These exceptions support the view that Dioscoreaceae should be thought of as drifting away from the ancestry of the Asparagoids, but not as drifting away from the ancestry of the Smilacoids. Moreover, Smilacoideae as climbing after the manner of *Petermannia* by tendrils are quite apart.

The left side of the large circle is the side of the rhizome; the other is the side of the coated bulb. The para-Dioscoreeae possess the rhizome and demonstrate that the rhizome must have passed through the proto-Dioscoreaceae. In the next paragraphs the reader will find the agreement between Asparagoids and the rhizomatous Dioscoreaceae illustrated, and at p. 344 the manner of evolution in the Dioscoreeae of their tuber which was manifestly an advance after the Dioscoreeae had appeared.

Monocotyledons delegate their business with the soil to the lower end of their stems. These ends must have surface enough for the carrying of a sufficient number of roots and bulk enough to handle the business of converting to use what the roots bring to them. This adding of bulk includes space for storage; and in the rhizome it is done without interfering with that property of stems of elongating, though great plagiotropism is introduced, controlled responses to gravity, light, etc. The para-Dioscoreeae and the Asparagoids march together, as if the property of elongating may not have been interfered with until the Dioscoreeae had come into being; and that was assuredly when the proto-Dioscoreaceae had become superseded.

The left side of the large circle is also the side of petioled leaves. The proto-Dioscoreaceae most certainly started with petioled leaves; further elongation of the petiole and its delicate pulvini must have followed the adoption of twining, i.e. must have commenced at the first steps of the Dioscoreaceae.

The massing of the flowers which is very marked in the Dioscoreeae does not occur in the Asparagoideae; and it does not occur in the para-Dioscoreeae and so may be assumed another feature of late appearing. It accompanied a reduction in size of the flower.

The transfer of assimilation to phylloclades in the Asparageae is a puzzling development; but the rest of the Asparagoideae are normal and it is not until the contrast of fleshy and dry fruits is under consideration that a little hesitation arises.

Though elongation of the connective cannot be admitted as evidence of an alliance between *Asarum* of the Aristolochiaceae and *Trichopus*, it can be admitted as one among a collection of characters which afford evidence of affinity between *Paris* of the Asparagoideae and *Trichopus*.

The diagram (Fig. 10) suggests the origin of the Stemonaceae to have been from the proto-Liliales in the neighbourhood or climate of the origin of the Dioscoreaceae, and of the relationship of the two families there is more to say here.

A century before any of the para-Dioscoreeae were known, *Stemona* had attracted attention: a dried specimen from Madras had been sent to the India House in London and passed to Petiver for report. Petiver allowed Plukenet to use it for a figure and Ray was able to enumerate it in his *Historia plantarum* (1704). Two years after Ray's work was in print Rumpf had died in Amboina leaving in manuscript an account of a *Stemona* which had come to him in that remote island. Nearly a century later Loureiro found in Indo-China what he described in his *Flora cochinchinensis* (1790) as *S. tuberosa*. Loureiro's contemporary, Roxburgh, at that time a surgeon in the northern part of the Madras Presidency, obtained material of the species which Petiver had had, and his drawing of it received the name *Roxburghia gloriosoides* when in Banks's hands on its way to publication. The name is variously assigned to Banks, to Banks's librarian, Dryander, and to the Calcutta judge, Sir William Jones, and was issued without the application of Loureiro's name being known. Roxburgh, after having been transferred to Calcutta to take charge of the Botanic Garden, received into cultivation more of the plant—this from Chittagong, and he sent some of it into gardens in London where it flowered, but did not fruit. Sir James Edward Smith described and figured it from one garden (*Exot. Bot.* pl. 57, 1807) and Sims from another (*Bot. Mag.* pl. 150, 1812). Smith, who sometimes used the Linnaean System and sometimes the Natural, wrote that there was no difficulty in assigning it to the Asparagi of de Jussieu; Sims wrote strangely that it fell between the Liliaceae and Asclepiadaceae. It is curious that Lamarck repeated this very superficial comparison. Reichenbach next assigned *Stemona* to the Taccaceae (*Consp. Reg. Bot.* p. 44, 1828). Roxburgh had figured the fruit on a scale so small as to be of indifferent value; Lindley on this account wrote out to Calcutta for fruits in spirit and had excellent figures made which he passed over to Wallich for publication in the latter's *Plantae asiaticae rariores* (pl. 282 with text on p. 50, 1832) and he set up the family Roxburghiaceae with the misleading remark 'it approaches the Araceae more than anything else'. The date of this was approximately that of assigning *Trichopus* to the Aristolochiaceae, and the suggestion equally astray; but he quickly realized that he was wrong and withdrew it (*Nixus*, p. 23; 1838). Griffith in 1844 endorsed Lindley's first statement but seems to have been unaware of the withdrawal. He had studied the plant in the Calcutta Botanic Garden (*Calcutta J. Nat. Hist.* **4**, 239, 1844). Lindley on withdrawing his suggestion of affinity to Araceae brought *Stemona* alongside *Dioscorea*, *Smilax*, *Luzuriaga* and *Philesia* and others into the group which under his name Dictyogens he composed of Roxburghiaceae, Triuridaceae, Dioscoreaceae, Smilacaceae (his limited Smilaceae——Smilacaceae no. 3), Philesiaceae (i.e. *Philesia* of the Liliaceae), and Trilliaceae (i.e. *Trillium*, *Medeola* and *Paris*), using the netted venation of the leaves and structure of the stem as his definition. Though his proposal obtained little support, it had done the service of bringing the Dioscoreaceae and Asparagoideae together. In 1837 Endlicher's *Genera plantarum* began to appear; and that excellent taxonomist was puzzled by *Stemona* (as *Roxburghia* must be named); the morphology of the flower was under debate. Roxburgh had called the lower part of the stamen 'a nectarial body'; Smith had rightly called it filament; Endlicher said it was a member of the perianth to which a stamen was attached, a statement which Eichler called surprising. This body is rendered unusual by a prolongation of the connective and that brings it into one view with the para-Dioscoreeae and the few species of *Dioscorea* which have apiculate anthers. Endlicher made two suggestions of affinity, one to Smilacaceae i.e. to Smilacaceae no. 4 which contained a series of genera from the Asparageae of others; and a second of affinity to *Gloriosa* (he used the synonym *Methonica*) which is somewhat of a stretch, as *Gloriosa* is a plant close to *Lilium*. Griffith's account of *Stemona* had been written before Endlicher's, but was published after it, partly in the *Calcutta Journal* and partly in the *Posthumous papers*. In 1869 Baillon made a more valuable contribution; he had studied the development of the flower (*Adansonia*, **1**, p. 255), had seen the four members of the perianth appear decussately two by two, then the four stamens together; and he had seen this curious sequel that when the pollen-sacs became evident their upper half was sterilized and with that the connective rapidly extended itself into the strange process until the four together plugged the entrance to the flower and protruded beyond its mouth when it had opened. There exists a curious paper (Lachmer-Sandoval in *Bot. Zbl.* **50**, 65, 1892) in which the author makes the unbelievable claim that they hinder pollination. A renewed study is suggested. Baillon, while likening the monocarpic ovary to that of *Calla* and *Arisaema*—species of the Araceae—emphatically rejected Lindley's suggestion of an alliance with *Luzuriaga* and *Philesia*. He and everyone else accepted Stemonaceae as a family, but Hooker, in accepting, recalled *Paris* in the Liliaceae-Asparagoideae, as having the parts of the flower in fours likewise. This alteration from the expected 3 to 4 is certainly a fact to be kept in mind but it is not repeated in Dioscoreaceae.

Stemona is one of the Liliales with a half inferior ovary. Bringing to mind the absoluteness of the sinking of the ovules into the top of the pedicel in Dioscoreaceae, one wonders how far it is likely that *Stemona* started out of the proto-Liliales along with the proto-Dioscoreaceae and fell behind. A modern tendency with the taxonomists is to diminish the importance given to the position of the ovary in arranging the Monocotyledons. Massive progress from superior to inferior is not suggested as for the Dicotyledons; and the sequences of the last century which sharply divided the Monocotyledons into inferior ovaried and superior ovaried are now regarded as cutting across the phylogeny.

The last family—the Taccaceae—placed on the left side of the diagram, comes up here for mention. Queva claimed this family to be closest to the Dioscoreaceae (*Mem. Soc. Sci. Lille* (4), **1**, 4 and 39, 1894). It is certainly close, though perhaps Stemonaceae is closer. Its affinity with Dioscoreaceae is seen in the vascular plan, the anatomy of the seed-coats, the broad stigmas, the broad connectives, the free-ended nervules in their leaves and the well-developed petioles. Lotsy in 1911 (*Vorträger bot. Stammungsges.* **3**, 923) placed Taccaceae immediately after Dioscoreaceae and Burmanniaceae immediately after the Taccaceae; and he mentioned Smilacaceae as the probable ancestors of the Dioscoreaceae. On his p. 863 he prints a phylogenetic diagram obtained from Hallier in which a common origin is postulated for Taccaceae and Burmanniaceae out of the Asparagoid Liliaceae, but a direct origin of Dioscoreaceae from Smilacaceae, meaning by the name no. 4, the Smilacoideae, which as already explained is not possible.

In 1912, in a long paper (in the *Arch. néerl. Bot.* (4), **1**, 146–234) he revived Endlicher's Artorhizae and added Burmanniaceae to the Dioscoreaceae and Taccaceae which had constituted it. Endlicher's proposal is a recognition of genuine affinity, but Lotsy's reorganization is not recommendable.

It is to be remarked that Taccaceae, Stemonaceae, and the Parideae of the Asparagoideae are conspicuously eastern in their modern dispersal.

Nepenthes is eastern along with the few para-Dioscoreeae; the section Stenophora shows that rhizomes in Dioscoreaceae have their greatest development in the East. These suggest the origin of the Dioscoreaceae to have been in the East. If so, this suggests that proto-Dioscoreaceae (eastern) divided into para-Dioscoreeae (eastern) and Dioscoreeae (pantropic).

Lindinger, in 1910 (*Naturwiss. Wochenschrift*, **25**, 65), called Dioscoreaceae atavistic.

He was assuming the Monocotyledons derived from the Dicotyledons and from that deduced a return towards Dicotyledonous characters in leaf and stem. They are not degenerate and the accusation of being atavistic seems to be wrong. Süssenguth, in 1919, with a great wealth of data claimed Dioscoreaceae to be primitive among Monocotyledons. That also must be wrong; they are neither primitive nor ancestral to any other family. Though the dwarf species be recessive as to ability to grow that does not make the family atavistic.

Enough has been said to show that the Aristolochiaceae have no connexion with the Dioscoreaceae. The Burmanniaceae are much nearer by reason of their connexion with the Taccaceae; but they have no actual connexion with the Dioscoreaceae.

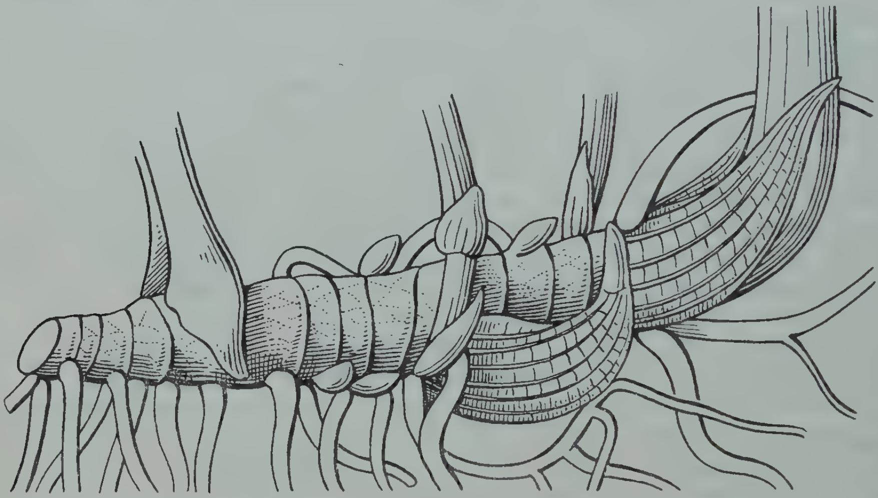

Fig. 11. The rhizome of *Aspidistra elatior* Bl.; from the *Tijdschrift voor Naturlijke Geschiendenis*, tab. IV.

III. MORPHOLOGY AND MORPHOGENESIS

§9. *The stem carried by an adult plant above ground*

It is a family character that the stem is annually displaced and replaced. Can it last more than a year? Perrier de la Bâthie described his *Avetra sempervirens* as having a persistent stem. Dr Hauman, giving an account of *Dioscorea multiflora* of the section Sphaerantha, as observed in cultivation at Buenos Aires (*An. Mus. naç. B. Aires*, **27**, 458, 1916) called the stems evergreen and seems to wish it to be understood that they outlast the year. There are strong reasons for holding that in these plants the stem does not continue active through a second year.

With perennial humidity, as in Upper Assam, *D. wattii* is virtually evergreen as it sends up a new stem at the time of the death of the old. A slight extension on this would allow an observer to regard the stems of *Avetra* and *Dioscorea multiflora* as perennial.

My attention has been directed to the note of a field collector in Mexico who claimed that *D. bartlettii* would branch in the following year from the stem of the earlier year at 40–75 feet above ground. This is incredible. All in all, a 12-month may be taken as the approximate limit of the life of an aerial stem in the family, for the next stage beyond 12 would be 24 months, by a jump impossible of attainment.

In the other direction there are Dioscoreas whose stems are above ground for only 6 months; but none have been shown to be above ground for a shorter time. The duration, consequently, may be said to be boxed in between the periods of 6 and 12 months.

A climate that does not provide reliably to give these perennials at least 6 months of adequate humidity and warmth is not habitable, and assuredly never was. Dwarfing comes with the occupation of land affording no more; climbing is attained with rather more time and competition with evergreen forest requires 9–10 months in which to grow. We do not possess good records: observers are ready to refer to the height of the shrubs, etc., climbed over, but do not measure the climbing stems. Miège, however, has measured his *D. mangenotiana* as 40 or more metres. The biggest Dioscoreas cannot spread over the top of the forest in the way that giant species of *Vitis* do; and this is because the stems are not perennial.

Dioscoreas are always advantaged by openings in the forest where streams break the canopy and when trees fall. But they seem never to smother their hosts, though they doubtless weaken them.

The dwarfs are of two kinds, those of the rocks and those of the savannahs. It is obvious that the latter species are such as have close relations in thin forest from which they have moved, their seedlings being less repelled by greater exposure to sun. The Madagascan *D. hexagona* is the most interesting of them. Its nearest relative, *D. soso*, grows among trees; but it grows among grasses, though, should the position of an individual plant be near a bush and the soil be a little more humid; it twines on the lower branches of the bush with the ends of its stems. Africa, the continent which has developed such a profusion of terrestrial orchids, seems to be driving another species, *D. quartiniana*, in the direction of occupying savannah. There has been no parallel evolution in Asia; but some in the New World. These savannah Dioscoreas tend to have narrower leaves than the Dioscoreas of the rocks which is in keeping with the way in which the shadows fall; *D.* (*Borderea*) *pyrenaica* is typical of the rocks. An ability to make very rapid growth is a character of the larger species; it is done with great economy of material and the stem is slender. The character of twining partly depends on this.

A plant which twines cannot begin the twining until it has length enough for circumnutation. Therefore the extreme dwarfs cannot twine as they cannot effectively circumnutate. The larger species invariably twine. There are two developments that a twiner has superposed on its circumnutation; the one is a greater horizontality of the movement; the other the sensitivity which checks the growth on contact and is diatropic in action. The quality of twining has been acquired by so many unrelated families of plants that it is safe to believe that the Dioscoreaceae originated their own arrangement. There is no reason why it should not vary, being the more effective, the more rapid the rate of growth. It is, for instance, weak in the xerophytic *D. elephantipes* being confined to its more slender branchlets.

A further character of the stem is that it provides a great profusion of axillary buds and, in spite of that, branches very sparingly. The buds come under apical dominance; the more active the apex the tighter its hold on them. Therefore branching is driven towards the time when the apex weakens. Exceptions to this are few; one is in *D. rotundata* which, low down, produces stiff diatropic branches looking as if they would arrest the stem from slipping downwards in a thicket (Fig. 12).

Except under abnormal circumstances, and that only as far as we know in two species of the section Lasiophyton, there can be no flowers formed until the majority of the leaves have been spread in the light. One of these two is *D. hispida*, which in a damp cellar starts growth, when growth is due, without soil and will put out a number of inflorescences but keep leafless, the sex observed being always male. The other is the plant called in herbaria *D. kamoonensis* var. *praecox*. It would seem that its male plants can behave in the same way.

Normally flowers on all plants are distal and on all but dwarf plants carried in branches which are entirely committed to flowering.

Bulbils are whole branches committed to their purpose and like the inflorescences distal. They, both in size and number, are a family character.

Orthotropy is a character belonging to the whole stem, and is responsible for keeping the lower part erect and straight; twining overcomes it, but when twining fails to fix its curve the orthotropism reasserts itself. There is profit in the absence of the urge to twine over just so much of the stem as can maintain itself upright. In the history of the family this upright portion began the annual race for light in which the twiner, starting from the soil, had to reach at least the lower branches of the support by the time that their weight was increased by leafing, but could only do this by the strictest economy of material. Out of this economy came the slender stem, paying out leaves on whose assimilation to profit and very greatly in need of their work, at first inhibiting all growth in their axillary buds.

Increased length however, was achieved and that led to competition with taller Angiosperms and an ability to obtain positions in the deeper forests of the humid tropics. Problems of growth forced reproduction towards the end of the season, whether sexual or asexual reproduction, and a delayed dispersal of seeds made the service of the wind profitable before the family spread from a subtropical life to tropical forests. All along the history of progressive size there had been the possibility of slipping out of the struggle against the growing trees by accepting the shade of rocks instead, though this involved accepting inferior conditions at the soil. This led to dwarfing. Borderea and the Andean dwarfs illustrate this. The dwarf *Trichopus* does not: its case is altogether peculiar. The Andean dwarfs are witnesses to very long climatic stability with trying conditions; *Trichopus* to still longer climatic stability but with overpowering forest.

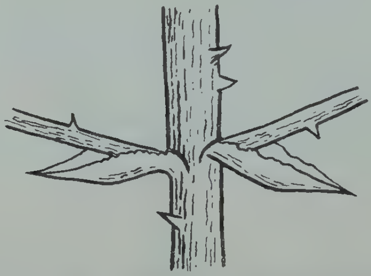

Fig. 12. The diageotropic position taken by a pair of branches low down on the stem of *D. rotundata*, useful for arresting a possible slipping earthwards when the stem is ascending free through a tangle. Nat. size.

It may be assumed that the climatic régime under which *Trichopus* evolved has not been repeated; for no similar evolution has come over Dioscoreaceae subsequently.

Stem-twiners commonly have rough stems, purposely to prevent slipping; the roughness in the Dioscoreaceae takes the form of longitudinal ridges; the size of the circumference determines how many; where the stem is in contact with its support it is sufficiently horizontal for them to cross the direction in which slipping could occur. We do not need to regard them as called out to strengthen, though they may be found strengthening by holding collenchyma and they harden the surface in many species for the carrying of prickles while the grooves between them provide shelter suitable for glands. The ridges invariably overlie vascular bundles. The phyllotaxy depends on the width of the apex where the leaves originate; the bundles called common because they pass from the leaves to the stem, depend for number on the phyllotaxy; and the ridges are dependent on the bundles. Thus is the number of the ridges determined at the apex.

Inversely in *Dioscorea alata* there are wings over some bundles but not over others, the wings descending from the bases of leaves. The bundle does not call out the wing, but where a wing is to appear, it will be over a bundle. Assimilation in *D. alata* is the wing's function.

Ridges, wings, prickles and glands are specific characters unlikely to expose remote history: the method of building up the vascular system on the other hand must expose history. The straight courses of the bundles caught the attention of anatomists of von Mohl's time because they expected a curving inward and then outwards which is the path in the palms and others. The investigator will find this curving very marked in the genus *Smilax*. He will find it in the thick main stems of *Asparagus officinalis*; but in the thin side branches of the latter he will find a single circle of straight bundles suggesting *Dioscorea*. It is convenient to leave further discussion of this until later (see p. 355).

During the stem's effort to attain the greatest possible elongation, the very pronounced apical dominance has held back branching, but has lost power when the branches appear committed to flowering and therewith to leaflessness. There is a suddenness in the appearing of inflorescences worth study as connected with the senility of the apex of the stem; they elongate late and they never attain diameters in any way approaching the diameter of stems that carry leaves. The flowers themselves only terminate the smallest of axes.

The greatest diameter recorded is 4 cm.: this astonishing diameter, recorded by Prof. Miège for his *D. mangenotiana*, must be the diameter of an underground part of the stem (see p. 360) and it is quite out of the ordinary. A diameter of 1 cm is thick for a typical *Dioscorea*. Species which alter this diameter just above the soil taper upwards; some with thinner stems at the base thicken upwards to the first assimilating leaf. The gradual thinning upwards is connected with the upward passage of something bound up with the food supply. As the stem thins the leaves that it bears, finishing their growth, cease from growing in an advancing degree. Goebel, devising the term heteroblasty for the leaves, could have applied it also to the stem. A branch committed to be a bulbil or an inflorescence is in another category; its elongation is reduced but not by heteroblasty, though doubtless partly by its lateral position.

§10. *The direction of twining*

The direction of twining which in the Higher Plants is widely a generic character, is a sectional character in *Dioscorea*. This Uline discovered.

Botanists have so extensively confused the expressions—twining to the right and twining to the left—that it is necessary to state that I use them as an observer sees the growing stem in front of him: the twining is dextrorse if it mounts, as he sees it, towards his right hand and sinistrorse if it mounts towards his left hand. As explained the direction of climbing is the direction of circumnutation. Doubts have been expressed as to the taxonomic value of the direction; but as to the Old World there can be none, for the direction almost without exception characterizes an entire section. It appears to be not quite so absolute for the species of the New World, but approximate enough for use with caution. I pass on to recorded exceptions.

Schenck (in Schimper, *Mitt. Tropen.* **6**/**1**, 123, 1892) states that a plant of *D. elephantipes* in the Berlin Botanical Garden twined in both directions but in different parts. Herbarium specimens of the African *D. baya* have been observed to twine sinistrorsely whereas the character of its section is to do so dextrorsely (Burkill in *Proc. Linn. Soc. Lond.* **151**, 60, 1939). Observations in the field are required to prove if this could be a local lapse on a normal plant. The Siamese *D. inopinata* of a sinistrorse section has dextrorse twining. Uline states that the Andean *D. humilis* climbs in both directions; we know that the pedicel may be coiled in both directions when the plant forces the fruit into the soil, the second being that antidromous coiling which is readily seen in tendrils with fixed ends; and I think that this is what he refers to.

There is one section only in Asia which twines to the right, the section Enantiophyllum; there are three in Africa, the sections Enantiophyllum, Asterotricha and Cotinifoliae: there are thirteen in America, scattered through the genus if Dr Knuth's classification be followed; eight are relatively herbaceous—Dematostemon, Hyperocarpa, Trigonobasis, Centrostemon, Cycladenium, and Choristogyne; five have distinctly woody stems—Cryptantha, Strutantha, Macrothyrsa, Sarcantha and Periandrium. These five are all of one brotherhood and could be assembled into a single section without flying in the face of any characters; their male inflorescences are spikes or spike-like racemes; their seeds are winged all round like the seeds of Enantiophyllum and Asterotricha. The eight are not of one brotherhood, the sections Trigonobasis, Centrostemon and Cycladenium and Monadelpha run together; they have water-storage in their flowers in varying degree. The section Dematostemon stands apart. Right twining, furthermore, has been attributed to two sections in which left twining occurs. Using the section as the unit for measurement, right-twining increases from east to west, and in the present unsatisfactory state of knowledge of the species of the New World looks a less reliable character in the New than in the Old World. Taxonomists have put a left twiner into the right-twining section Apodostemon. Uline could not bring the section into line.

Sinistrorse twining is the commoner in the plant world and is in the genera of the Liliaceae—*Asparagus*, *Semele* and *Herreria*—in those of their species which twine.

The circumstance that left twining is the commoner in the plant world has made Knuth suggest that it was the original direction in the Dioscoreaceae. So it may have been. The para-Dioscoreeae exhibit both—left twining in *Stenomeris*, right twining in *Avetra*.

§11. *The base of the annual stem*

As already said, when the Dioscoreaceae edged their way from the rest of the proto-Liliales they had a rhizome. When this rhizome branched, usually it was to send up an aerial stem: the ascending stem would pass through a little soil before it was exposed to the air and this short length constituted the second part of the stem underground, the first being the rhizome. There is so little to say about this short length that is below ground that it may be said and disposed of at once. The stem is transformed into the exposed part so abruptly as to make it beyond dispute that its nature is controlled by the darkness and the humidity in which it grows. The cortex is swollen and wholly of undifferentiated parenchyma; the stele is also swollen by parenchyma. The surface never carries prickles. It may carry hairs as sometimes the rhizome does; but to carry anything on the surface is unusual.

The similarity of absence of sclerenchyma from this bit of undergound stem to absence from the cortical part of a tuber suggests that the surface of the latter is ruled by the darkness and humidity of its underground position. This bit of underground stem may be of more than one internode. It may or may not root at an internode which happens to be within the soil. If it does so, the roots do not have the strength and length of roots from that node below it by which the aerial stem and rhizome or tuber are united—the node of the perennial bud.

It has been shown (*J. Linn. Soc.* (*Bot.*), **53**, 328) that this short length of stem in *Tamus communis* turns on its own axis in growth (see p. 353 below). This turning is apparently part of the process by which the direction of the Genetic Spiral enters into the phyllotaxy.

§12. *The ancestral rhizome becomes a tuber*

Botanists owe to Ker-Gawler the term rhizome. He borrowed the word from the pharmacists, used it for the horizontal swollen perennial stem of Irids which travels on or just below the surface of the soil. The term has suffered so much from loose use that it is essential here to state in what way it is to be taken: it implies (i) cauline nature; (ii) horizontality and (iii) thickness. That which has not all three is not a rhizome. The underground stem of *Paris quadrifolia* (Fig. 14D) is not a rhizome but a stolon, for it has no thickness: the underground stem of *Aspidistra* (Fig. 11, p. 340) is a rhizome for it has all three qualities. Both genera belong to the subfamily Asparagoideae of which subfamily the tribe Aspidistreae has, in particular, characters that reappear in the para-Dioscoreeae. The Asparagoid *Paris quadrifolia* is a depauperate extreme. Fig. 13A, the rhizome of *Dioscorea nipponica*, is a very successful species of today.

The latest German morphological text-book calls the tuber of *Tamus communis* a 'vertical rhizome'. It is time to abandon this confusion. It is not an innovation for we find it in print as far back as 1835 when Dutrochet wrote of *Tamus* 'the tuber is a subterranean stem... such as physiologists call a rhizome', adding 'it grows vertically instead of horizontally'. He did not name the physiologists to whom he referred; on the contrary, von Mohl only a year later called the storage organ of *Tamus* a tuber.

About this time, which was the time of the great distress due to disease in the European potato crops, *Dioscorea opposita* (*D. batatas* Decne) was introduced from China for trial as an alternative for the potato; and because Dutrochet had called the tuber of *Tamus* a rhizome, Decaisne gave the same morphological rank to the structurally similar tuber of *D. opposita*, writing: 'reproduces by its roots or to speak more exactly by its rhizomes...genuine underground stems which instead of creeping under the surface of the soil drive themselves perpendicularly downwards (*Rev. Hort.* (4), **3**, 243, 1854). Duchartre challenged this and declared the tuber a root (*Bull. Soc. Bot. Fr.* **1**, 201, 1854); Germain de St Pierre who had germinated bulbils and had seen a tuber appear as a swelling at the first node underground, declared it to be a root because roots occur in such a position.

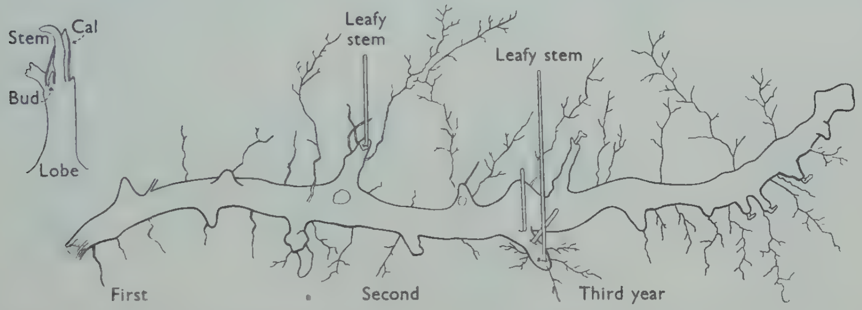

Fig. 13. The living part of a rhizome of *D. nipponica*, which in 10 years had advanced a metre before increasing shade of an evergreen *Berberis*; reduced to $\frac{1}{4}$. Also one of its lateral branches, natural size, showing a bud breaking through its calyptra (*cal.*); the month August. The roots on the left were dying.

D. opposita soon produced seeds in Algeria; and Duchartre was able to obtain and to germinate them. His paper (*J. Soc. Imp. Centre Hort.* **4**, 467, 1858) is interesting, but he mistook the parts of the seedling and stated the tuber to be axillary to a presumed second cotyledon. The next observer was De Bary (*Vergl. Anat. Vegetat.* **3**, this being the third volume of Hofmeister's *Handbook*, p. 640, 1877) who touched off a persistent error by declaring that the Dioscoreaceae have storage organs of three kinds, namely swollen roots, rhizomes and tubers formed by the swelling of the first internode of an aerial stem. The swollen root was his own interpretation of the tuber of *D. opposita*; the rhizome was genuine, being that of *D. villosa* which had been in gardens in Europe from before the days of Linnaeus, and the third was derived from what had been written about *Tamus*. It is curious that Sachs added his great authority to De Bary's interpretation of the tuber of *D. opposita*, yet in a different manner. Sachs called his material *D. japonica*, and as *D. japonica* is the parent of the cultigen *D. opposita*, he was working virtually with the same material. He gave out that the tuber is a root that has lost its root-cap. Though his work seems to have been done about 1880 in the course of studies on polarity, the conclusion was not given out until 1893 (*Abh. Pflanzenphys.* **2**, 1220) and then without reasons for it.

The reader will recognize that if De Bary and Sachs had been right, the view taken in this paper that the tuber in the Dioscoreaceae is a contraction from the rhizome would be wrong. Moreover, if the storage organs in the family were of three origins, the evolution of the family from the proto-Liliales by a single line would also be wrong. But until now central Europe has followed De Bary without question.

The correct view is: (i) that the rhizome, as the proto-Dioscoreaceae received it, was required to increase its storage tissue, and it thickened; (ii) the thickening took the form of making it stouter and then plagiotropically lobed, and (iii) the stoutness produced difficulties in driving a way through the soil in which burial was essential for preservation; (iv) at the same time the effort to climb as high as possible made it profitable to nourish only one stem; and aerial stem production was therefore limited to the active front end of the rhizome; (v) the shortening of the rhizome followed; (vi) the enlargement of one or at any rate very few plagiotropic lobes was favourable. By this means a tuber displaced the rhizome. A subsequent and novel line was the transfer of the greater part of the storage space from the shrinking rhizome to plagiotropically swollen lobes deeper in the soil and therefore better protected.

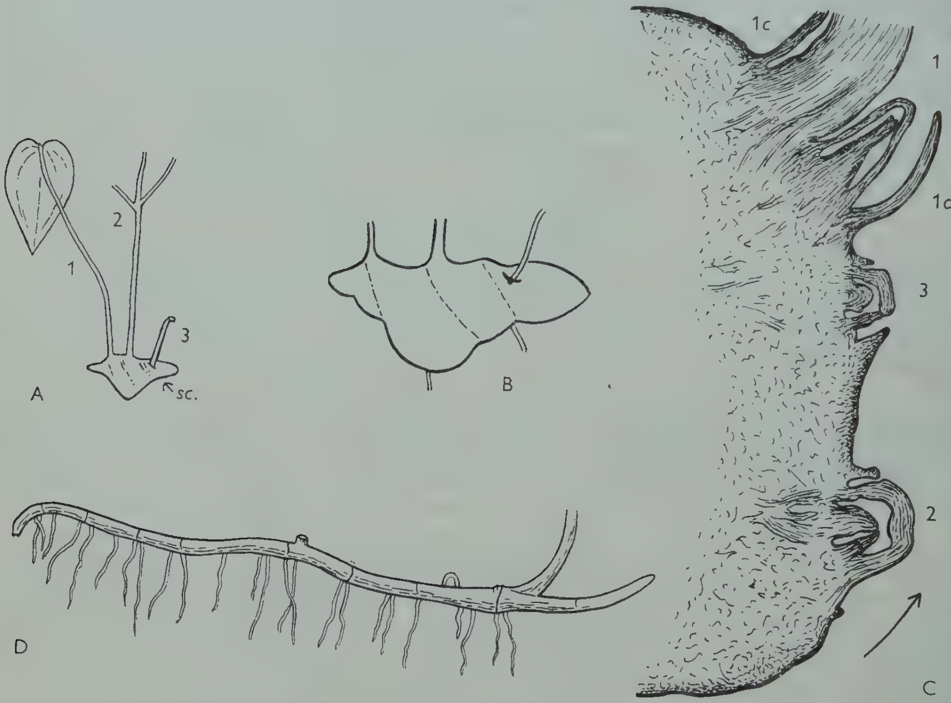

Fig. 14. A, the rhizome at 5½ months of *D. villosa* (nat. size); 1, the first assimilatory leaf, 2, and 3, the succeeding aerial stems; *sc.*, a scale leaf. B, the rhizome, × 3. C, A vertical section through the blunt end of an old rhizome of *D. glauca*; 1, 2 and 3, its crowded buds, the oldest has burst through its calyptra (1*c*.) and a lateral bud had been produced in the axil of the calyptra: a layer of cork covers the surface between the buds. Secondary growth will rotate this in the direction of the arrow. D, The stolon of *Paris quadrifolia*, half nat. size.

Fig. 14A shows the plagiotropic lobing appearing on a seedling of *D. villosa*. The seedling though only 5½ months old was giving rise to its second aerial stem and later might carry a greater number than this each year. Fig. 14C is a section through the apex of the rhizome of the allied *D. glauca* with three buds which will be turned upwards by plagiotropic growth below them, as the arrow suggests.

It is not improbable that the extremely liberal production of buds and the severe winters of climates into which Stenophora extends are connected; for the severe winters would seem to take a heavy toll of buds. If that be so the evolution of the tuberous Dioscoreas with their limitation in the number of stems would be expected to have taken place away from severe winters.

Nature has not preserved the intermediates between rhizome and tuber; it would be natural for that which is neither the one nor the other to be lost.

As yet seedlings have had too little attention; but there is an account of that of *D. villosa* by Holm (*Amer. Midl. Nat.* **9**, 458, 1925). A germinating *Dioscorea* immediately prepares for rhizome or tuber; it grows out in some part of the hypocotyl;[1] or it seems in *D. pyrenaica* to use the whole hypocotyl for conversion into a tuber. In *Tamus* and *Dioscorea elephantipes* growth is a lobe arising out of the hypocotyl. In the rhizomatous Stenophora, it seems (but needs confirming) that the growth seizes the epicotyledonary side. Fig. 14A shows the rhizome of *D. villosa* at 5½ months with a plagiotropic swelling deeper in the soil than the place of origin of aerial stems. The accompanying figure (Fig. 13C) is a vertical section through the apex of the rhizome of the allied *D. glauca*—its several buds ready to be turned upwards. Fig. 15 represents tubers of *D. cayenensis*, each consisting of a head which represents the rhizome, and a parenchymatous storage area which represents the plagiotropic lower swelling of Fig. 14.

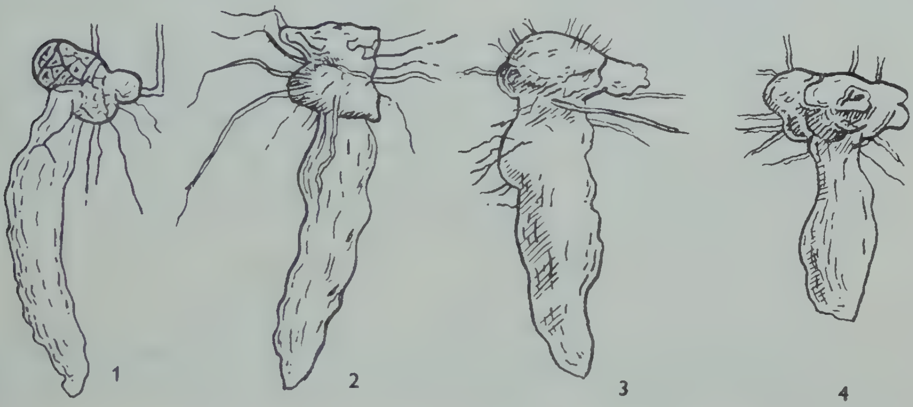

Fig. 15. Four tubers of *D. cayenensis* showing the woody corm above the fleshy storage tuber, from a photograph by Dr J. Hutchinson. ×⅕.

In Guinea a new development has appeared in the section Enantiophyllum: in it this hard cormous head, representative of the rhizome, sends out horizontal branches from the apex of each of which an aerial branch ascends. The device separates to a little distance from one another the several stems which the plant can produce yearly; and makes a mat that protects the plagiotropic food-storing lobes. The upper surface of the horizontal branches is covered by cork. In 1947 the Linnean Society published for me 'A plea for a description from life of the African *Dioscorea minutiflora* Engl.' (*Proc. Linn. Soc. Lond.* **150**, 79) which contained a restoration of the underground parts made from herbarium scraps. Miège has recently described and figured the underground parts of his species, *D. burkilliana*—a species of affinity to the material which I used—and the reader is referred to his interesting paper (*Bull. Inst. fr. Afr. Noir*, **2**, 48, 1958). Dr Miège graphically describes the surface exposed upwards as 'a woody tray'. In a slightly earlier paper (*Rev. Bot. Appl.* **30**, 423, 1950) he had figured and described how the horizontal branches of *D. minutiflora* may be extended as branches of normal thickness, but with the nodes swollen into callosities which can put out roots and give origin to separate plants when the stem behind them decays. The reader is referred to his paper for a description of them. These species from Guinea get, by planting offsets, exactly the same advantages as the ancestral rhizomes gave of mobility, and *D. minutiflora* has recovered the possession of rhizomes; the tuberous fingers below them are plagiotropic lobes. The structure is of great interest and incidentally suggests how evolution may be tortuous.

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[1] Karl Reiche whose description of the germination of *D.* (*Epipetrum*) *humilis* is referred to on p. 328 makes no mention of the hypocotyl of this species, though he states that there is a bud which aborts, between the cotyledon and first assimilating leaf. His description is suspected of inaccuracy.

A still more curious underground system is found in the South American *D. dodecaneura* which Queva discovered. One might call the discovery disturbing.

Underground hairs occur in an interesting way on both rhizomes and tubers when they are very young. Goebel in 1905 announced that he had found them on the tubers of *D. opposita* and *D. japonica* and on the rhizomes of *D. quinqueloba*, by which name he may have meant *D. nipponica* (*Flora*, **96**, 183). He called them 'root-hairs': Van Tieghem, following, called them more accurately 'hairs functioning as root-hairs'. If Sachs had seen them, possibly they were part-cause of his assumption of a root without a root-cap. I figure such hairs (Fig. 51 D on p. 387) from the underground parts of *D. dodecaneura*.

Queva's work had preceded Goebel's, but followed De Bary's. He, in regard to material, was as thorough as possible, examining as many species as he could get together in Lille where the Municipal Garden of the city provided him with whatever was available from the horticultural establishments of western Europe; and he drew also on what he could get from Buitenzorg in Java and the Jardin des Plantes in Paris. He spoilt the excellence of his undertaking by accepting any name that reached him; and this compels me to enumerate what he had and what he called it.[1]

I take up the history of *D. dodecaneura* in cultivation to show how it got its several names.

Otto had brought a garden form from South America and had grown it in Berlin as *D. discolor*. Kunth published the name in 1850 as his own; and under it the plant reached various horticultural institutions. Linden made a second introduction and scattered various new names for such clones as he could distinguish. The firm of Bull of Chelsea did the same, and from the operations of all three the species now exists in clones sparsely but widely distributed. Seeds have not been forthcoming and a study of the germinating plant remains desirable.

Its clonal or asexual reproduction is by clavate bodies which have the shape of the tubers of *D. esculenta*, *D. arachidna*, *D. orbiculata* and others, i.e. in appearance they are commonplace; but internally they are not. When the time of new growth comes the peduncle is dead and an adventitious bud has formed at the tuber's distal end. The peduncle is a root in structure. Queva saw this and claimed also the presence of a root cap over the end, deeper than which he found the adventitious bud to be organized with a cork layer over it. He described the tuberous body carefully; it might be a root he argued, writing 'the nature of the apical meristem leads one to think that the tuber is a swollen root, but the structure of the bundles and their orientation is in opposition to such an interpretation and leads to admitting that they are stems' (p. 367). Queva then made a claim that he had seen an admixture of stem and root in material of '*D. repanda*' (i.e. in *D. pyrifolia*) and in an unidentifiable taxon that he called *D. kita* and in *D. batatas* (i.e. in *D. opposita*). *D. pyrifolia* and *D. opposita* belong to the section Enantiophyllum and, as already recorded, *D. opposita* had been claimed to have root tubers by De Bary and later by Sachs. It is unfortunate that Queva did not give in any way how stem and root were mixed together, and so left merely for conjecture what it was that brought him into a measure of agreement with De Bary and Sachs.

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[1] Queva's material enumerated by sections: Stenophora: 1, a species probably *D. glauca*, called by him *D. villosa*; 2, *D. quinqueloba* which was raised from seed for him. Combilium: 3, *D. esculenta*, by tubers from Java under the name *D. aculeata*. Opsophyton: 4, *D. bulbifera*, by bulbils from Java and also by bulbils from Madagascar through Paris. Lasiophyton: 5, *D. hispida*, by seed from Java under the name *D. hirsuta*; 6, *D. pentaphylla*, likewise from Java. Lychnostemon: 7, *D. amarantoides*, which had been brought into cultivation in Belgium as *D. multicolor*. Enantiophyllum: 8, *D. alata*, from Java, as *D. javanica*; 9, *D. opposita*, under the then accepted name *D. batatas*; 10, *D. pyrifolia*, from Java as *D. repanda*. Brachystigma: 11, *D. sinuata*, from cultivation in Europe, both by this name and as *D. variifolia*. Lasiogyne: 12, *D. dodecaneura*, from cultivation in Europe as *D. discolor* and as *D. illustrata*. Borderea: 13, *D. pyrenaica*, and 14, *Tamus communis*. Furthermore he used herbarium material to obtain a little information regarding the genera *Stenomeris* and *Trichopus*. The chief sources of his data were *Dioscorea villosa* meaning *D. glauca*, *D. bulbifera*, *D. hispida*, *D. opposita* and *D. dodecaneura*.

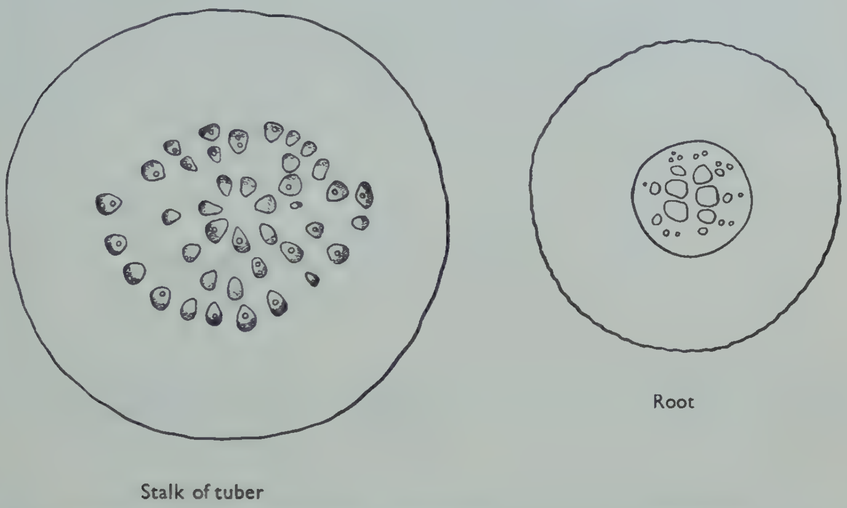

Fig. 16. Transverse sections through the reproductive body of *D. dodecaneura*, on the right through the root near its origin and on the left where swelling towards its greatest diameter.

Queva called Goebel's attention, as Goebel admits, to what he had seen, and the latter set out to look into the matter for himself. How he came by his material, he does not reveal. He astonishingly called it *D. eburnea* Lour. var. *fusca*. It had nothing to do with Loureiro's plant, but had come out of one of the introductions of *D. dodecaneura*. His account (*Flora*, **95**, 167, 1905) is interesting and his morphological deduction that the tuber is an organ 'sui generis', neither stem nor root, is arresting. He proceeds to draw the tubers of *D. opposita* and *D. japonica* into the same class, and then by a leap, scarcely supported, the bulbils of these, though they are obviously cauline structures.

While Goebel was occupied in verifying Queva's discovery, Leonhard Lindinger was working in Hamburg on the anatomy of the roots of Monocotyledons; and he published a paper in the same year as Goebel's in which he referred to *D. dodecaneura*, but only as regards its cortex. Goebel's paper sent him back to the plant to write his own account of the morphology underground (*Bot. Zbl. Beih.* **21/1**, 311, 1907), wherein he states emphatically that the pedunculate tubers are roots, because (i) they arise adventitiously at a stem node (a compelling reason) and (ii) are initiated at the endodermis; (iii) because they carry no more than repetitions of themselves, i.e. roots which though small are genuinely roots; (iv) because they have a complicated zoned stele surrounded (v) by an endodermis of thick-walled U-shaped cells—not a compelling reason; and (vi) they terminate in a root cap. The endodermis fades out where the swelling begins and the stele, invaded by parenchyma, breaks into scattered meristeles each with its xylem and phloem, in number more than the earlier parts of the peduncle promise. The swollen part acquires the anatomy of the swollen tuber which is a stem-structure in other Dioscoreas. The cork at its end is a curious interrupting layer in its growth; it drives the renewal of growth to be endogenous. Would any part of the swelling, lateral to the tip, originate endogenous buds if the terminal were destroyed? It has become very desirable to look further into the morphology of this unexpected structure which cannot be brought into line with the underground parts of the Old World Dioscoreas.

I have already called attention (p. 347) to Karl Reiche's claim that it is the primary root that tuberizes in *D.* (*Epipetrum*) *humilis*; his work should be checked when the germination of *D. dodecaneura* is followed. Fig. 16 is from a plant which had reached the Royal Botanic Gardens, Kew, as *D. discolor*.

If *D. dodecaneura* and *D. humilis* so depart from the expected, are they the only American species which do so? I have wished to get seeds that the seedling might be studied, but have been unable to arrange for that.

Observations on renewal of growth in the germination of the tuber of *D. dodecaneura* indicate that the bud from under the cork-enclosed apical end does not directly produce an aerial stem, but that its second node is the base of the new plant; there it sends out two kinds of roots differing in thickness; the thicker to tuberize distally as described. Both kinds of roots have root-hairs. Its business being to send up an aerial stem in due time it travels near the surface; but Goebel found it in one case to grow to a length of 2 m. (*Flora*, **95**, 181). Where this organ on swelling breaks up its vascular bundle it does what the stout stem of *D. sansibarensis* does and what the swelling of the normal cauline tuber does. If we assume that this breaking up is entirely the result of swelling and say, with Lindinger, that the whole organ is root, though where swollen the root characters have been destroyed, we are still in face of a taxonomic difficulty, for tuberized roots in the Liliaceae occur in the Asphodeloideae and we have been claiming the Dioscoreaceae allied to the Asparagoideae.

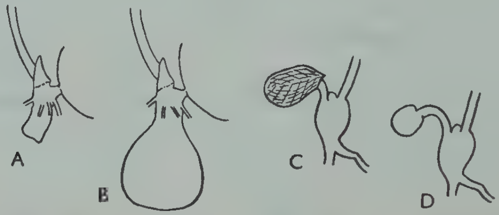

Fig. 17. A and B, two stages in the formation of a new plant of *D. bulbifera* from a bulbil. C, a newly germinated seedling of *D. pyrenaica* showing the stalk of the cotyledon to be long enough to adjust the position of the hypocotyl. D, the same with the cotyledon uncovered.

There is nothing in the tubers of *D. dodecaneura* to suggest a node. In this the rhizomes of the Stenophoras are in contrast; their closely packed buds (see Fig. 14) show them full of nodes. The bulbils of all the Dioscoreas are equally with close-packed nodes. The tuber of *D. dodecaneura* is in contrast to both.

A bulbil is a whole branch side-tracked for reproduction, and bears comparison with the rhizomes in particular which cut down their many nodes to subscribe to the welfare of the one stem that successfully grows into the air.

Parenthetically it may be said that there is need for a full account of the origin of the rhizome in a germinated Stenophora; Goebel's account of the germination of *D. quinqueloba* (*Flora*, **95**, 170 with a figure) does not go far enough. Can the rhizome, it needs to be asked, proceed from any other part of the seedling than the epicotyledonary end of the hypocotyl?

To the best of our knowledge stem cuttings of Dioscoreas never take root. Why should they? The stems are due for early death. Bulbils as a rule do not root though their early death be circumvented; but we do not know for how long. They put out a shoot; and it is the shoot which roots from its first node, doing this contemporaneously with tuber-production. I figure here (Fig. 17) the tuber forming in *D. bulbifera* and refer the reader to figures of the forming tuber of *D. sansibarensis* in *Blumea* (*J. J. Smith Jubilee*, **1**, 232, 1937). As the tuber forms, the bud of the first node is appropriated by it as its perennial bud. Could better evidence be asked for the cauline nature of the tuber than this? Positive geotropism rules the direction of the new tuber's growth and it is demonstrable that it circumnutates equally with the stem when it has length enough, by-passing thereby stones and other impediments encountered in the soil. The way in which a long tuber curls itself in a flower pot which is too shallow for it, exposes its circumnutation; and it can be seen that this is in the same direction as that of the aerial stem.

The capacity of a tuber is increased by lobes; as the forming tuber in Fig. 17, these lobes are not branches. Such knowledge as there is at present does not allow the position of a lobe to be any more predictable than the position of a new head, should the leader be destroyed.

The shape of the tuber whether in massive connexion with the corm or on a peduncle, is indisputably a result of natural selection against herbivores whose depredations may be checked by deep-burial.

§13. *The bud underground and dominance of one bud over another*

The reader is referred back to Fig. 14C (p. 346) which shows the crowded buds of new stems at the apex of the rhizome of *D. glauca* and to the statement in the text that a reduction in the number of buds would be to the plant's advantage if thereby fewer stems brought longer growth to those left. So it was. The shortening of the rhizome until it became a tuber and the strengthening of an apical dominance in that tuber worked together to make the reduction, which we see so often at its ultimate state—a single stem arising from a tuber that has been resting. The stem during rest had been the oldest axis in the oldest bud of its neighbourhood—twice over at the head of a phalanx of axes. Thus is provision made against mishaps.

The individual bud consists of a sympodial system held in arrest by that oldest unit which alone will be enabled to grow. When it grows it 'bolts', and turns into a stem, gives origin to leaves and lays down buds—one, two or three in a column—in every axil and then immobilizes them by its apical dominance; but it gradually loses restraining power as it loses ability for further growth and as that happens branching begins. This is why all branching is distal. From the horizon at which branching is permitted down to the soil the inactivated buds have lost power; but under the soil is the one exempted—the perennial bud that released the stem of the annual cycle now ended. Because it is exempted it makes a class of its own.

It is convenient to make a classification of all the buds by their performance: (i) the perennial bud which stands apart; (ii) those able to grow, if liberated, into repetitions, of the parent stem; (iii) those which when liberated end with partly arrested elongation, becoming bulbils; and (iv) those committed to bear flowers and unable to follow the stem in any way.

There are two ways in which the perennial bud is constructed: (i) that of the rhizomatous species, and (ii) that of the tuberous. The difference is attributable to the foundation, for the rhizome grows in length under the forming bud and draws it into a zigzag, whereas the other does not have its spirality disturbed. Figs. 18–20 have been prepared to make the difference clear to a reader prepared to agree to these two postulates—(i) that its direction of growth is centrifugal so that each emerging bud in turn loses its central position; and (ii) that the bud is invariably on that side of its parent axis which is towards the centre of the whole system, i.e. towards X in the figure. Because each emerging bud requires as much of the available space as possible in which to be laid down, their initial arrangement is distichous. This arrangement is not continued for long because it is not economical of space, so that, by displacement of buds, distichy is converted to tristichy. It is not undirected displacement, but some inherent quality determines that the displacement shall be towards the position *W* in Figs. 18 and 19 instead of towards *Y*. A genetic spiral results, which is subject to further displacement in the buds that are drawn into a zigzag.

It is possible to argue that, the zigzag bud being a complication of the straightforward spiral bud, the section Stenophora in which it occurs does not have a rhizome which is really ancestral. Alternatively, the pulling into a zigzag may not be general in the Stenophoras. Further research is desirable.

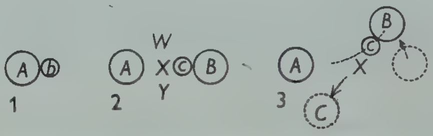

Fig. 18. Diagram of the initiation of the spiral underground perennial bud. *A*, its first axis with its axillary bud (*b*) (the calyptra is ignored as confusing the diagram without adding information). In the second component, growth in the foundation by inserting tissue at the centre of the field (*X*) has parted *b*, now growing to the size of *A* (and shown as *B*). The combined repulsion between *A* and *B* and *B* and *B*'s own bud *c* drives *B* towards the position *W*. The successive repulsion causes the bud to be built up as a third component with spirality now evident and the position of *X* fixed.

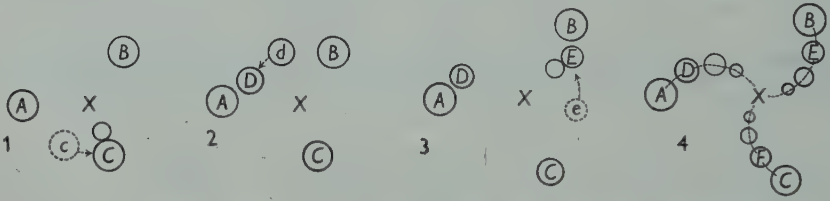

Fig. 19. The further extension of the bud on the plan; following on from Fig. 18.

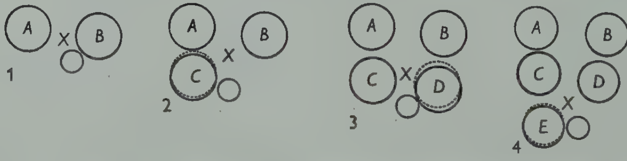

Fig. 20. The building up of the zigzag bud with the position *X* moving under it.

The bud in the rhizomatous species is large and loose; that in the tuberous species small and close-packed. Preparations show under the microscope the cavities between the organs to be full of mucilage with colleters on the surfaces: this mucilage has been derived from colleters disrupted in preparation or earlier natural accidents.

The components of Fig. 21 are from microtomed sections, and their proportions are exact. Component 1 is transverse through the base of a bud of *Dioscorea glauca*; 2 is transverse through the base of a bud of *D. sansibarensis*; in the latter as the foundation is humped, the first axis is cut so much above its base as to have lost size and so appear small in comparison with the second; component 3 is a vertical section through a bud of *Tamus communis* and component 4 through a bud of *D. nipponica*. The axes are lettered, as in the Figs. 18–20, from *A* forward and the calyptrae by small letters—*a*, *b*, etc. The reader will note that the space between the calyptrae is much less in *Tamus* than in the other three: he must be informed that *Tamus* is typical of the majority of the species of

Dioscorea that I have examined. I think that in it and in the Dioscoreas with close-fitting calyptrae the apical dominance of the first axis is stricter than in the others. The reader by laying a ruler over component 1 of Fig. 21 will observe that it is impossible for a section to pass through every axis, and then he will understand how it is that component 4 of Fig. 21 misses axis A, while its calyptra (*a*) is present, hooding *B* and all that follow. In passing, attention may be drawn to the plug which closes the top of calyptra *a*. The section is not quite medial through axis *B* and is marginal for most of the axes. The stoutness of axis *B* should be noted for it illustrates how the Stenophoras have stems that are thick—actually thickest—at the very base. So, too, are the stems of *D. sansibarensis* thickest at the base. It is interesting to observe in component 2 that axis *C* inclines towards the position *Y* in Fig. 18, component 2.

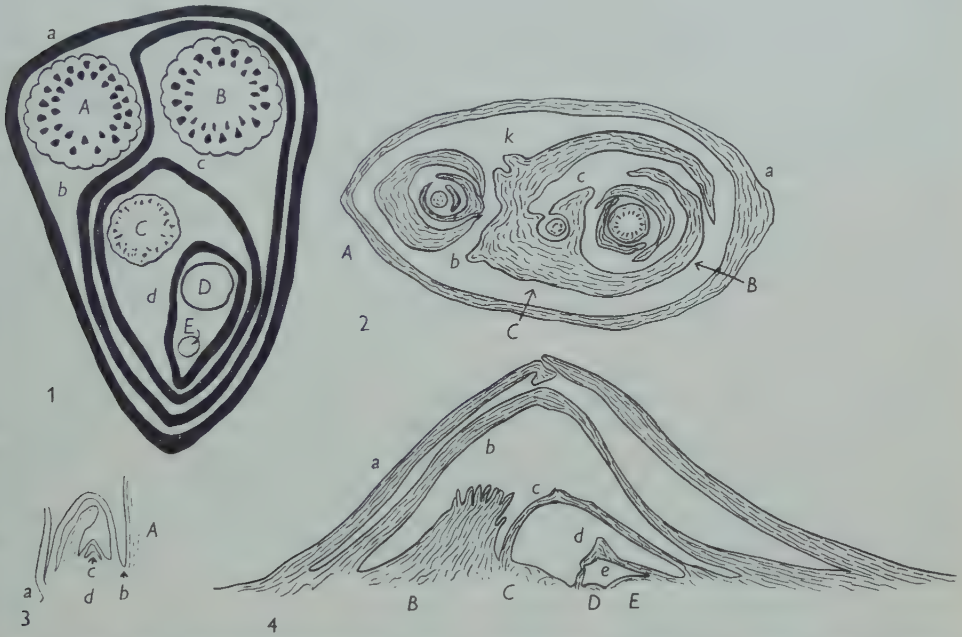

Fig. 21. Sections through the perennial bud: 1, transverse through the emergences of *Dioscorea glauca*, 2, through the base of the bud of *D. sansibarensis*; 3, vertical through a bud of *Tamus* and 4, a bud of *D. nipponica*, *A*, *B*, *C*, etc., the successive axes; *a*, *b*, *c*, etc., their calyptrae; *k*, a false keel produced by the foundation rising under the calyptra as it often does in these buds where there is room for this to happen. The calyptra of axis *B* is folded round the axis, whereas the calyptra of axis *A* encloses the whole bud.

I have not detected suppressions of axes within the perennial bud.

In *Tamus* the aerial stem has to force its way upwards through a few centimetres of soil, and this forcing leads to an exposure of the fact that the stem twists on its axis whereby the scale leaves within the soil are folded back and down in the direction of the genetic spiral by friction with the soil (see the figure in *J. Linn. Soc.* (*Bot.*), **53**, 328). Another reference may be made, namely to Fig. 18 on p. 352 of this paper—in which the passing of axis *B* towards the position *W* is of a similar nature.

§14. *The surface of the aerial stem: its prickles, colleters, etc.*

Colleters, hairs and glands function physiologically; prickles serve for protection against larger animals, and correspondingly they are produced by larger Dioscoreas. The prickles are crowded together where they may lacerate the snout of the rooting animal such as a wild pig. A dozen species of the section Enantiophyllum, roughly limited to the wettest lands of the Far East, have the whole of the lowest few centimetres of the aerial stem coated with the prickles, the armature beginning abruptly where the stem breaks through the soil and ceasing rather rapidly upwards, the last prickles being at nodes. Where these Enantiophylla grow, a small number of species of other sections are well armed in the same part of the stem with the same diminishing of the armature upwards.

The much sparser prickles higher up the stem afford less protection; but they may save stems from being broken when associated, as they are in *D. lamprocaula*, with such a toughness that an animal of some size, pressing against the stem, may drive a prickle or two into its skin. *D. lamprocaula* is also of the section Enantiophyllum and is spread from northern Indo-China to and through Malaysia. *D. esculenta*, which guards its tubers by thorny roots, has prickles higher up its stems.

All prickly stems need bands or layers of rigid thick-walled cells as support for their prickles.

It is not to the gain of the plant which protects its tubers by them that they should be spread to a distance away from the tubers; and as the horizon at which they abruptly appear is determined by emergence from the soil, the lowest internode should have no power of continuing elongation but rapidly harden itself and them.

In a few species odd prickles appear on the back of the petiole and still more rarely on the back of the midrib of the leaf. All the species which bear them are such as have great vigour; and the appearance of the prickle seems exuberant. The prickles rise above vascular bundles and their occurrence will be recalled in connexion with stipules (see p. 376).

I defer my discussion of hairs to p. 386 as their association is closer with leaves than with stems; but it is convenient to discuss colleters at once. They are general within the vegetative buds to an extent which makes it more interesting to find them absent than present. As the leaves of a bud expand they become disorganized and their mucilage spreads over the nearest surfaces. A bruise before a bud's expanding fills it with freed mucilage. Exposed surfaces never renew the supply; but the fore-runner tip of *D. sansibarensis* has two creases on its upper side within which the supply is maintained for the harbouring of nitrogen-fixing bacteria. Prof. Miège has found something similar in another African species—his *D. mangenotiana*. Both are described on p. 385 onwards.

Very young leaves and parts of the stems close to the base of these leaves, in a variety of species, give origin to internal glands, each from a single epidermal cell which proliferates inwards. These glands are discussed on p. 383.

§15. *The interior of the stem*

The internal anatomy of the stem provides characters of phylogenetic importance, which go far towards assuring us that it was by a single line that the family took origin, for the whole family is one in them.

These anatomical characters are as follows: (i) the 'vegetative line' of the axil for every leaf above ground is short; (ii) the number of bundles passing through the line is three; (iii) the median of the three, which of course is that which becomes the midrib of the leaf, leads inwards to a ganglion whence, as if by rebound, it descends the stem at a right angle; and (iv) keeps at a constant depth below the epidermis; (v) the two laterals of the three skirt the ganglion, make a connexion with it; and (vi) take the right-angle bend to make the downward course in the stem keeping parallel to each other, to the central bundle and to the epidermal surface whatever the distance be that they travel; (vii) in the ganglion two bundles originate which, by their source, are liable to be a little deeper in the stem than the three common to leaf and stem; (viii) these—the cauline bundles—have a course strictly parallel to the others, descending the stem on either side of the mid-common bundles (see Figs. 24 and 25, p. 357–58). The alternation of common and cauline bundles—sometimes called pectination—is a consequence of position of origin and subsequent parallel course. Out of the eight characters just enumerated, the vegetative line, the ganglion and the straight courses of the bundles appear to have been evolutions dating from the appearance of the family, the ganglion the most original of the three.

I take the reader back to the year 1831. In that year Hugo von Mohl published his first investigations on the courses of vascular bundles in the Palmae. He pointed out the manner in which the many bundles which in them pass the vegetative line penetrate in a curve to the neighbourhood of the centre of the stem and then reverse towards the surface of the stem. In a second paper of 1845, extending his observations considerably, he cautiously suggested that this—the palm-pattern—might be a monocotyledon pattern strongly developed in the palms and less developed in the rest of the Monocotyledons. Next, after the Palmae, he placed the arborescent Liliaceae and stressed the resemblance that he had found between the genus *Dracaena* and the palms. Of the botanists who took up his line of work after him, Nägeli and Falkenberg need to be mentioned. Nägeli published in 1858 the results of very extensive investigations into the course of bundles (*Beitr. wiss. Bot.* **1**, 1) including among the plants studied *Dioscorea opposita* (*D. batatas*) and *Tamus communis* (pp. 123–129).

He called the ganglion a ‘fibrovasal mass’, but failed to realise its importance, inserting it in one diagram and omitting it from another: the course of the bundles was uppermost in his mind. Falkenberg followed in 1876 (*Vergl. Unters. Bau. Vegetat. Monocotyledonen*) with a study perhaps a little wider. Nägeli, Falkenberg and later also Chrysler (in *Bot. Gaz.* **38**, 161, 1904), as well as a few others, provide evidence that bundles penetrate into the pith in the following families: Typhaceae, Pandanaceae, Gramineae, Cyperaceae, Araceae, Bromeliaceae, Zingiberaceae, Cannaceae, and Orchidaceae, in addition to Liliaceae and Palmae. As the inclusion of Liliaceae is, to the argument here, of first importance, it is necessary to ask in what subfamily and genera of that family this is the case: in the Asphodeloideae (*Xanthorrhoea*), Allioideae (*Allium*), Lilioideae (*Lilium*, *Tulipa* and *Fritillaria*), Dracaenoideae (*Dracaena*, *Aloe*), Asparagoideae (*Asparagus*, *Ruscus*, *Convallaria*, *Aspidistra*), Ophiopogonoideae (*Aletris*), Melanthoideae (*Uvularia*) and Smilacoideae (*Smilax*). Curved bundles are therefore rather widely present in Liliaceae and a list of them includes several genera of that subfamily, the Asparagoideae, which I have suggested is nearest to the Dioscoreaceae of the subfamilies of Liliaceae.

Schwendener in 1874 (*Das mechan. System*, p. 75) had associated curved bundles with massive apices: the plant anatomists whom I have quoted had associated them with Monocotyledons. Schwendener was right: the accent is not on Monocotyledons but on the massive apex. As support for Schwendener is Falkenberg's demonstration that curved and straight bundles occur in different parts of the same plant in agreement with the size of the stem, for he showed that the thick stem enclosed within the bulb of *Allium*, *Lilium* and *Fritillaria* holds curved bundles and the aerial thinner stem does not. He figures it clearly in a diagram of *Fritillaria*. I am able to add that the thick stem of *Asparagus officinalis*—the part of the plant that is eaten—has curved bundles, but its branches have bundles in a ring and as straight as those of a *Dioscorea*. It is reasonable therefore to maintain that the Dioscoreaceae have no curved bundles because the bundles are pulled straight in the straining of the stem for length. Straight bundles are therefore a secondary consequence of the climbing habit.

Nägeli's and Falkenberg's studies provided De Bary with almost all that he had to say in his text-book regarding the course of the bundles. Falkenberg had claimed that the bundle mesh of the Dioscoreaceae has a relation to the palm pattern though he did not read evolution into his argument.

The reader will recall that the calyptra is amplexicaul (as is shown on p. 353) and the first foliar organ after it may embrace more than half of the axis. This comes to both of them from commencing with a priority of growth over the axis. In the palms the succeeding leaves retain the priority, but in the Dioscoreaceae the priority is at once reduced and the vegetative line of the axil falls to a very small part of the circumference of the axis, which rapid reduction is a part of the effort of the climbing stem to elongate as much and as economically as possible, and the small apex with the bundles straight is a part of this economy. If a palm pattern is to be recognized, so must be a dioscoreaceous pattern; but better a pattern for bulky apices and a pattern for slender apices.

Climbers have xylem vessels of large lumen which by their size facilitate the ascent of water through the reduction of the drag from the walls. The lumen is furthermore maintained by the sclerenchyma sheath against which the bundles run.

§16. *The internode*

Figs. 22–29 represent internodes of various species in transverse section, all but the first two drawn to the same scale. As an internode is very nearly a perfect cylinder the drawings may be taken as representing any part between the nodes. Figs. 22 and 23 are from stems which require greater magnification than the others. At a glance the cortex, the zone of the bundles and the pith are seen to be distinct from each other.

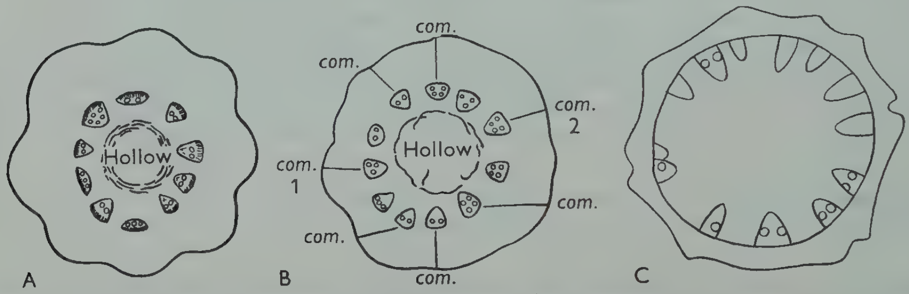

Fig. 22. The lowest internode of the two species of the section Borderea, × 9. A and B, *D. pyrenaica*; *com.*, common bundles; all ten bundles originated at the lower two nodes. C, *D. gillettii*. The ridges on the stem and the common bundles do not run well together.

The thickness of the cortex varies from species to species and within a species is increased on the part of the stem which is underground; the increase is in parenchyma, and whatever is underground is soft. Above ground the surface may be ridged, as some of the figures show. The ridges may be supported by collenchyma—especially where strength is needed for carrying prickles. A very pronounced endodermis defines the cortex inwards. The zone of the bundles begins generally in a girdle of sclerenchyma. The common bundles are often engulfed in it, while the cauline lie against and a little within it. If, as in *D. pyrenaica*, the cauline bundles are scarcely deeper than the common (see Fig. 22), dwarfing is the probable cause; and the same cause seems to be operative in the dwarf *Trichopus zeylanicus* (see E. V. Watson in *Notes Roy. Bot. Gard. Edinb.* **19**, 143, 1936).

Common and cauline bundles differ in obvious structural particulars and there is certainly a difference in what they do. Both are bilaterally constructed about the radius of the stem on which they are.

The pith is of undifferentiated parenchyma which breaks down in a few species, notably in those that are dwarfs, as *D. pyrenaica* and *Trichopus zeylanicus* and as several Madagascan species of rather small size, but also in large stems of *Dioscorea hispida*. In most species pith extends between the bundles; in many it invades them and makes the outline somewhat undefined. Whether within or between the bundles, it is a water-holding tissue which under pathological conditions may receive assimilates unable to make their way down the stem. If the passage down the stem is completely blocked, the pith may become quite full of starch.

Pectination, that is the alternation of common and cauline bundles in the ring, is determined as already explained at the nodes where two cauline bundles are originated in the ganglion to take their places in the space on either side of the mid-common, between it and the lateral common. This inequality of three to two is usually corrected a little down the stem by the elimination in a ganglion of one of the lateral common bundles, but not so early as to correct the want of parity at once, so that there is almost always in the ring one or more common bundles in excess and therefore one or more irregularities where two common bundles run side by side (see Fig. 27 B). They never unite nor break up except at a node; but they may lose size downwards, particularly the common bundles. The cauline sometimes are split into two at origin, but never during their course. Illustrations of split bundles are to be seen in Figs. 26 and 27. In *D. sansibarensis* the splitting may be so extensive that the bundle appears shredded. Splitting has been observed in the stems of *Tamus communis* where, though rarely, a descending bundle loses half to a ganglion that the other half passes (*J. Linn. Soc.* (*Bot.*), **53**, 337, 360), but this is not the same thing as the splittings here recorded: these are splittings at origin, for the nodal ganglion originated the bundles already split. Fig. 26 A shows six out of the seven cauline bundles in a distal internode of *D. sansibarensis* doubled in this way and Fig. 26 B shows five out of eight cauline bundles in an internode of *D. dodecaneura*: Fig. 27 A, the lowest internode of a stem of *D. sansibarensis*, shows cauline bundles in as many as five parts. This same figure shows the occurrence of Y-shaped cauline bundles embracing a common bundle. Presently I shall need to suggest that *D. sansibarensis* and *D. hemicrypta* are

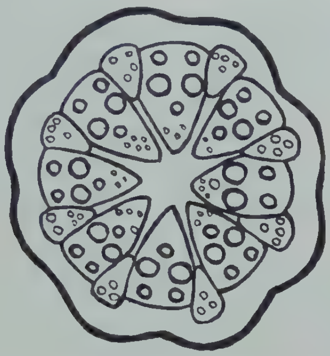

Fig. 23. Transverse section of an internode of *D. tsaratananensis*, × 20, showing how closely its bundles are packed.

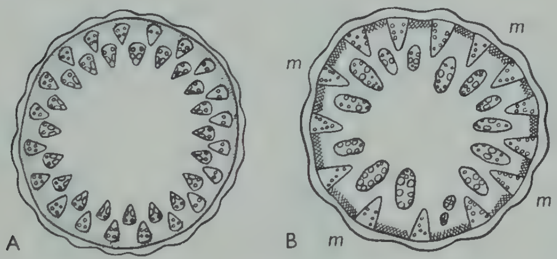

Fig. 24. The lowest internodes of two species of Stenophora showing their numerous bundles in two distinct rings, × 7. A, *D. caucasica*; B, *D. glauca*; *m*, median common bundles of four leaf-traces. The largest of the cauline bundles are those that have had the shortest course (cf. Fig. 25 B).

related to one another in a measure that gives colour to the idea that splitting of cauline bundles within the stem may be phylogenetically useful.

The splitting and regrouping in the fleshy storage organs ought to be compared when more data have been collected.

The section which supplied Fig. 27 A showed three zones of large xylem vessels, the largest vessels almost 2 mm. across and in the innermost ring. This suggests that the greatest amount of water is caused to ascend the stem towards its centre. As these large vessels are close to the proto-xylem it would seem that they are formed rather before the somewhat smaller vessels that are less deep in the tissues.

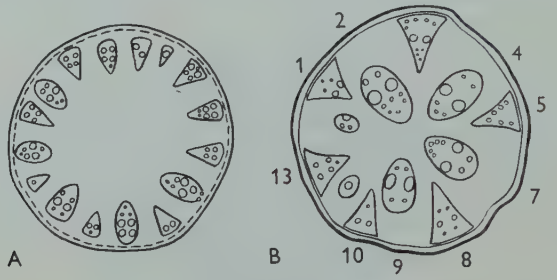

Fig. 25. Transverse sections of internodes of two species of Lasiophyton, × 7. A, *D. dregeana*; B, *D. pentaphylla*; origin the island of Rapa in the Pacific, with two cauline bundles greatly diminished; see the text, p. 357. Nos. 1–5 indicate the leaf-trace from the node immediately above the section; one bundle from the next node, no. 6, had been extinguished, the other four, nos. 7–10, are present; of the second node above, the mid-common, no. 13, and two greatly diminished cauline bundles persist.

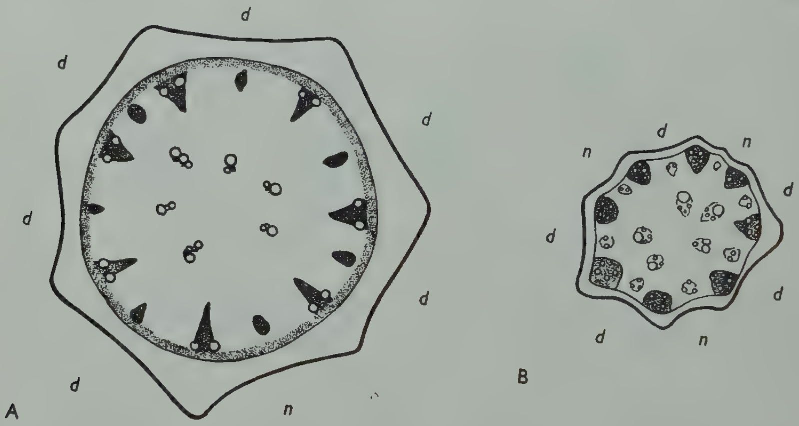

Fig. 26. Transverse sections of internodes with divided cauline bundles, × 7. A, *D. sansibarensis*, a distal internode of a vigorous stem showing six of the seven cauline bundles divided. B, *D. dodecaneura* with five of the eight cauline bundles divided. *d*, divided bundle; *n*, a bundle that is not divided.

It is very common for cauline bundles to have two groups of phloem and this possibly has had a place in evolving the splitting into inner and outer parts seen in Fig. 26. Von Mohl seeing two groups of phloem suggested the union of two bundles; but it is division, not union, with which one has to deal. Bucherer found three groups in the cauline bundles of *D. opposita*, two of them paired—right and left—so that one may say that there is an outer phloem group and a doubled inner group; and this is probably the best way of describing the position of the phloem.

Fig. 26 shows that in *D. sansibarensis* the opposed leaves need not be exactly opposite.

Fig. 28 is devoted to exposing a possible difference in the size and average number of the bundles in plants of *D. bulbifera* of different origins. Fig. 29 is devoted to *D. alata* which, in company with its nearer allies of the section Enantiophyllum, has a stem with alternate leaves at the base and passes over to truly opposite—decussate—leaves, with a possible return to alternation distally. Nägeli notes the same changes to occur in *D. opposita*. Decussation demands sixteen bundles; higher as well as lower numbers indicate a spiral phyllotaxy. No species has its number constant from the base of the stem to the apex; but some have higher numbers than others; and the range is taxonomic. The section Stenophora, for instance, is characterized by high numbers; and Fig. 21 shows how dense is the accumulation of incipient leaves in *D.* (*Stenophora*) *nipponica* on a stem about to emerge from the perennial bud.

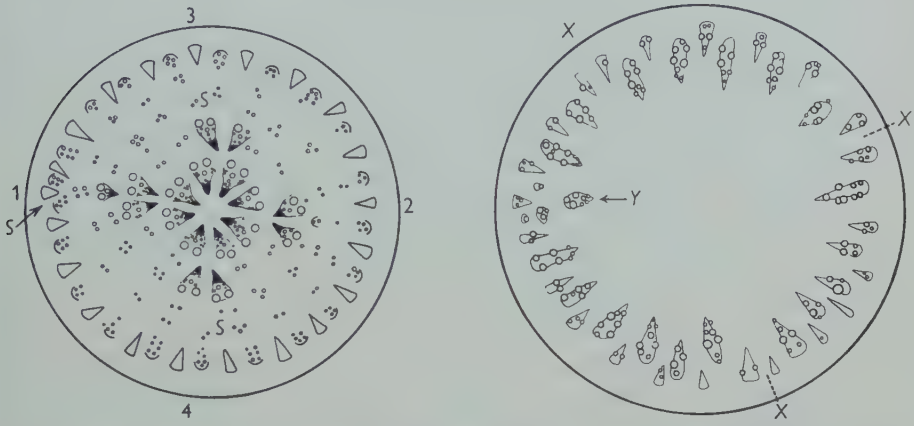

Fig. 27. Sections of the basal internode of two African species with particularly thick stems, × 7. On the left *D. sansibarensis*, on the right *D. hemicrypta*. The first four leaves in *D. sansibarensis* are paired, and the positions 1, 2, 3 and 4 receive their descending bundles; the cauline is shredded and contains very large xylem vessels zoned in size. At *S* the cauline fork to either side of a mid-common bundle. In the section of *D. hemicrypta* there is one similar case (letter *Y*). *X* denotes positions at which paired common bundles are seen.

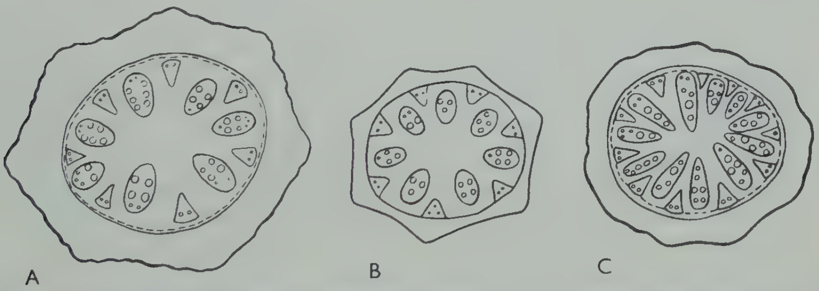

Fig. 28. Sections through internodes of *Dioscorea bulbifera*, × 7. A and B, the lowest internode and a distal node of the African var. *anthropophagorum*. C, through an internode of a plant from a bulbil obtained in Manipur, India. Both plants were raised at Kew under identical conditions.

Fig. 30 A shows the low number of the bundles in the upper part of a plant of *D. pyrenaica* where the pattern approached distichy. Dwarfing brings irregularities and so does apical death: the cauline bundles fail to appear and there cannot be pectination. The reader will observe that then as in component A of Fig. 30 three common bundles come

together; and if he will turn to the account of a dying tip of *Tamus communis* in the earlier paper (*J. Linn. Soc.* (*Bot.*), **53**, 364) he will observe an absence of cauline bundles to lead to the same irregularity.

There may be a physiological reason for dispersing the bundle elements in the interior of a large stem, which means that the stem of *D. sansibarensis*, as seen in Fig. 27, is, in this respect, an advance on that of *D. hemicrypta*.

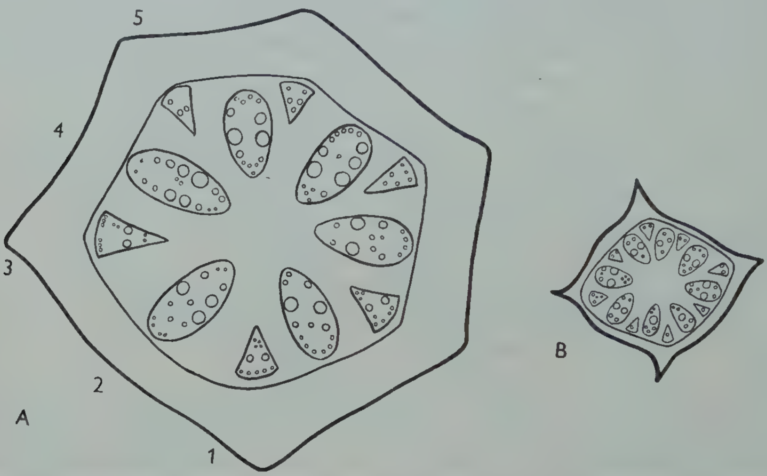

Fig. 29. Transverse sections through internodes of *D. alata*, × 7. A, the lowest, with thick cortex because underground, as well as spiral phyllotaxy. *B*, distal, with thin cortex and decussate foliage. The numbers 1 to 5 indicate the leaf-trace of the lowest leaf.

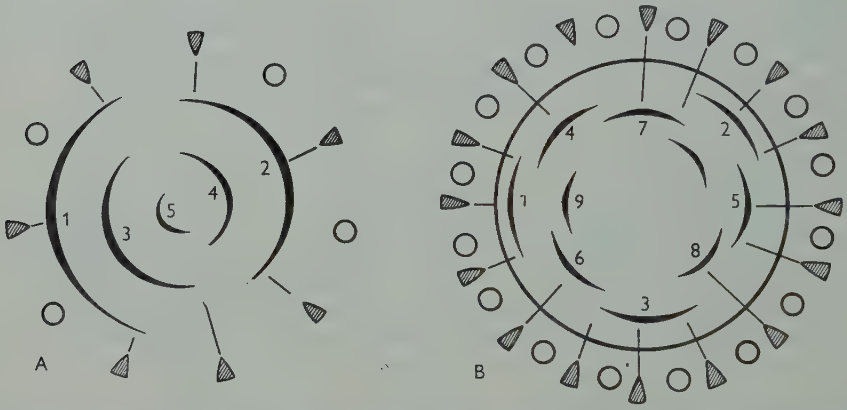

Fig. 30. Phyllotactic diagrams. On the outside of each the ring of bundles gives the positions of the common and cauline bundles, the two distinguished by their shapes; within the relation to them of the leaves whence the bundles descend. A is the basal internode of *D. pyrenaica*; the leaves are districhous except that no. 1 is not quite over no. 3, and a lateral common bundle escapes arrest at the first node. B is the basal internode of *D. glauca*, where with a greater size of stem, every leaf to the 8th is enabled to send bundles to the base of the stem. The bundles of the 9th leaf are lost in the nodes of the 1st, 4th and 6th leaves.

Falkenberg (*op. cit.* p. 156) wrote of the presence of tissue like cambium in the bundles of *D. villosa*; and Dr Agnes Arber has written (*Ann. Bot.* **52**, 87, 1918) of cambiform growth in the bundles of the family. It has not the persistence of real cambium, but is rather as it were, the end of growth and is not confined, in this form, to the Dioscoreaceae (see D. H. Campbell in *Ann. Bot.* **44**, 326).

§17. *The node*

Nägeli's reference to the ganglion as something resulting from union of bundles and Falkenberg's expression 'an imperfect knot' suggest that they gave it less importance than is its due. The ganglion is something that originates bundles, not merely a passageway as a consequence of their conjunction. They did not analyse it. It has four parts, one, the largest, behind three that are smaller. The largest is the ganglion proper; the three in front are the beginnings of the bundles entering the leaf; in the other direction they bury their end in the ganglion of an *older node*, having made but little union in their own. Sometimes two leaves are present in the mature stem at the same horizon (see Fig. 34), and therefore two ganglia; and though between them they may all but cross the stem they do not unite into a nodal plate. This independence is interesting and so is the closer connexion that a leaf has with the stem lower down than at its own horizon. The ganglion proper providing the two cauline bundles, neatly but quite naturally, places them between the cauline bundles and so completes the leaf-trace. T. G. Mason, occupied in research on transmission within the stem, wrote (*Proc. Roy. Dubl. Soc.* **18**, 198, 1936) that he found in the ganglion a plexus of interlacing vessels and two masses to a leaf of xylem prosenchyma overlying a number of phloem glomeruli. No writer has as yet unravelled the plexus which varies in complexity from species to species. It needs comparative study. Mason's observations were made on *D. alata*, *D. opposita* in the cultivated form '*D. decaisneana*' and *D. japonica*, all belonging to the section Enantiophyllum, on *D. sansibarensis* (he used the synonym *D. macroura*), of the section Macroura, *D. dodecaneura* (*D. discolor*) of the section Lasiogyne and *D. dumetorum* of the section Lasiophyton. In all of these he found the ganglion. Somehow he missed it in the section Stenophora and in *Tamus communis*; but it is present; and its shape in *Tamus* is figured in this *Journal* (**53**, p. 338). Mason found it to be particularly large in *D. dumetorum* (bilobed as in *Tamus*); and it was in the lobes that he found his phloem masses. I do not add here to our information on *Tamus*, but give the reader the benefit in Fig. 31 of work on the comparable species, *D. bulbifera*. Components A and B of that figure are transverse through its ganglion; A low down and B about the middle. As the ganglion slopes inwardly, there is little of its forward part in A, but more in B. It reaches back to touch two descending cauline bundles without leading to their extinction: these are seen in both components of the figure; the bundles that are extinguished—bundles which descend straight on to it—do not find a place in either component. The numbers on the diagram are given to common bundles, and letters are used for the cauline bundles. The ganglion is the meeting place of 1, 2, and 3 with *a* and *b*; its connexion with *c* and *f* is to be recognized as invasion as it is not invariable. Leaving component A for B, attention needs directing to the lower ends of the already half-extinguished descending bundles of the internode above, whose points appear at the back of the ganglion; and comparing the two components it is seen that one of the caulines among these is rather less absorbed than the other bundles, which is ascribable to its deeper penetration into the pith. Owing to the sinking of the ganglion towards the back the leaf-trace of the internode below the ganglion is all but assembled, and free in component A, freedom of 1, 2, and 3 appearing in component B in which a scarcely staining patch heads the cauline bundles above their actual origin. In component B the two bundles for the axillary bud are present, issuing from the ganglion on either side of bundle no. 1. It is easy to see how Nägeli came to regard them as part of the cauline bundles. Where the ganglion touches bundles *c* and *f* the xylem vessels are interrupted.

The reader will observe that the stem at the node is not round but somewhat elliptic. This is to be associated with the stimulus that produces a pediment under the leaf—a bracket, as it were, that strengthens the hold of the petiole and very slightly cuts the corner for the bundles entering the petiole.

Corrosion of the bundles *c* and *f*, if more extensive, would amount to extinguishing, and does so in parts of the plants where the number of bundles in an internode is increasing upwards.

The common bundles may be regarded as applied to the ganglion more than entering it. I add to Fig. 31 components C and D the better to show this: they show the section vertically through the ganglion of *D. sansibarensis*; component C is on the radius of the mid-common bundle and component D by the side of this radius so that it passes through a cauline bundle. As the reader will observe, component C is medial through an axillary bud and component D is tangentially near its margin: the mid-common, passing from the leaf to the stem, is seen to be well outside the corresponding bundle of its radius which is seen descending on to the ganglion. And component C of the figure shows how fluid passing through the gangion must take a *Z*-course—an argument for the ganglion being a pumping station. As the stem used for making the sections was a young one, the leaf at the node was still upright, and protective to the axillary bud. Another bundle to be noted is the commissural bundle between the ganglion and the nearby lateral common bundle. A pair to it, of course outside the section, would connect the ganglion with the other lateral common bundle entering the leaf-trace.

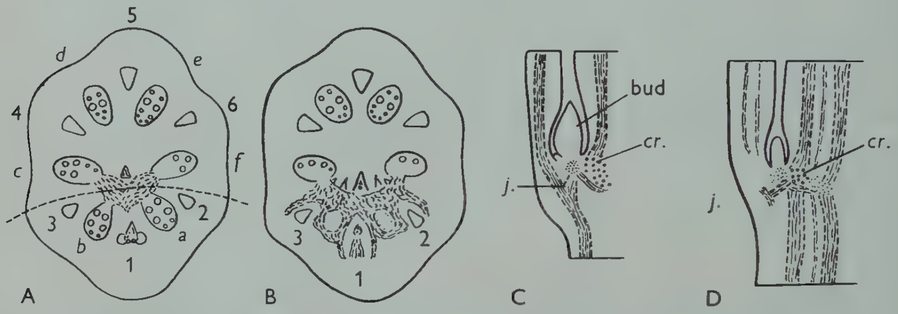

Fig. 31. The developing node; A and B, transverse through a node of *D. bulberifera*; C and D, vertical through a ganglion of *D. sansibarensis*. A is at a lower level than B so that all the bundles of the internode below it are seen; 1, 2 and 3 are the common bundles leaving the stem above; all the common bundles are numbered; the cauline are lettered. C is median on the radius of the axil; D is parallel to C: *cr.*, cross-over cells; *j*, junction bundle between the ganglion proper and a common bundle. The descending cauline bundle is shredded into three parts. Another descending on to the node also is shredded. Two buds are in the axil, medially cut in C, the larger tangentially cut in D.

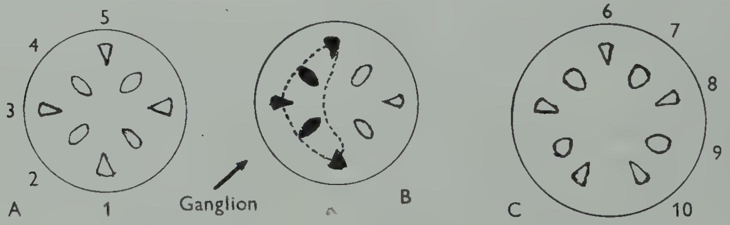

Fig. 32. Diagram of the lowest internodes of a thin stem starting with eight bundles, being an entire leaf-trace of 5 and 3 from the next leaf-trace. The stem, increasing in circumference, has nine bundles in component C. The second leaf-trace, composed of bundles 6–10, loses at the node no. 6 as it is extinguished in the ganglion where no. 5 of the first leaf-trace enters the stem.

It is convenient to think of the upper and lower faces of a ganglion as exposing the plan of the internodes above and below. The ganglion of *D. sansibarensis*, for instance, seen from below has long ridges that are drawn out into the cauline bundles. An anatomical examination points to a medial ridge between them. I have described the bundles as strictly straight, crediting their right-angle bend to the node. This does not indicate that I regard the right angle as homologous with the curve in the palm pattern: the palm pattern and the dioscoreaceous pattern are equally end-products in evolution.

The palm and the Dioscoreaceae patterns have this in common—that the mid-common in the palm pattern goes deeper into the stem than the others and towards its deepest slightly swells.

§18. *The prevailing phyllotactic pattern*

There are three phyllotactic patterns in the Dioscoreaceae; it is natural to take the commonest first and here follows a description of it. It has been misunderstood by taxonomists. At its greatest extension it begins with orthodistichy, passes into tristichy and returns to distichy. The passage from one to another is gradual: it depends on the diameter, one would say of the stem but actually of the stem immediately below the apex at the horizon where elongation sets in and overwhelms increase in diameter. In Fig. 33 is a section through the lowest internode of *D. opposita*, which shows the mid-common bundles of the lowest two leaves all but exactly opposite; that of the second leaf has slipped a little towards 12 o'clock of the diagram. This slipping back is the beginning of the genetic spiral and the amount of slipping will increase with the increase of the diameter of the stem. It is correct to accept Nägeli's discrimination of an up-spiral and a down-spiral side to the leaf-trace; and the spiral begins out of their difference. Fig. 30 diagrammatizes this, explaining how the second leaf-trace in a new stem is able to plant its down-spiral lateral common bundle in the ganglion over the point where the up-spiral lateral common of the first leaf makes contact with the ganglion.

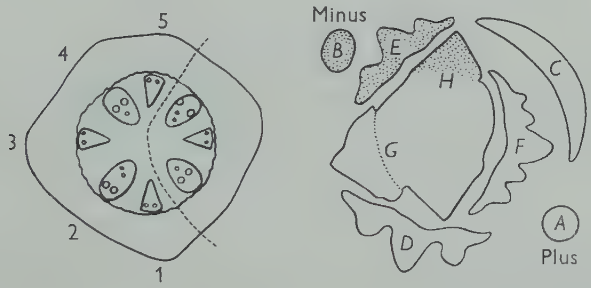

Fig. 33. *Dioscorea opposita.* On the left is the basal internode underground showing a thickened cortex; 1 to 5 are the bundles of the leaf-trace of the lowest leaf, and the three others are of the leaf-trace of the second leaf. On the right a transverse section through a vegetative bud, showing plus and minus sides; the letters indicate the sequence of the emergences. Explanation in the text.

The name Enantiophyllum was not given because leaves nos. 1 and 2 might be so nearly opposite, but because there are species in the section with decussate foliage (see on p. 366).

It is by no means uncommon for two leaves to stand at the same horizon and to be called 'opposite' in not strictly critical descriptions. Fig. 34 illustrates the case; in it leaves *A* and *B* have been brought to the same horizon by suppression of the internode between them: that they are not opposite is made evident because the whole of the leaf traces of leaves *E* and *C* have room to pass between the leaf-traces of *A* and *B* on one side, but only the leaf-trace of *D* on the other. Single bundles of the leaf traces of leaves *f*, *g* and *h* enter and pass beyond the horizon of the section so that eight leaves are represented. The 8th node down the stem is the most distant with which a leaf may make contact in this pattern, and the 5th the most distant node for the connexion to be by more than a single bundle.

The reader with this diagram before him will consent that the pattern is one of alternate leaves spirally arranged. His attention is directed to the circumstance that it is cauline bundles which represent the more distant nodes, not common bundles.

The stem from which this diagram was constructed showed that the two ganglia of the paired leaves did not approach each other at all and that there was nothing like a nodal plate.

Pairing of leaves is connected with that curious plagiotropy exposed in my paper on the stem of *Tamus communis* (*J. Linn. Soc.* (*Bot.*), **53**, 370) in which short internodes are connected with ganglia on one side of the stem and long internodes with ganglia on the other. The reader is now referred to Fig. 33, for which a vegetative bud of *D. opposita* was serially microtomed. This enabled the distances of foliar emergences from one another to be measured. A single camera lucida outline drawing suffices to illustrate what was ascertained from the series. Leaves A and B were cut by section through the petiole; A was at the top of a long internode, B at the top of a short one. C was cut through the base of the blade and topped a long internode. E and F and also G were cut through the lamina higher up; E topped a short internode, the other a long (relatively long) internode. G and H were not yet detached from the stem; but H was, so to speak, treading on the heels of G and promised a short internode. The whole bud showed that the parastichy of B–F–H was a minus one.

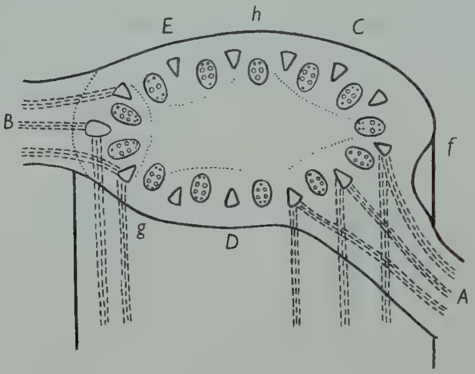

Fig. 34. Diagram showing the vasculation in *D. cayenensis* at a doubled node. Leaves *A* and *B* contribute their leaf-traces unbroken; the leaf-trace of *C* by-passes them unbroken: those of *D* and *E* each lose a lateral common bundle; only a single bundle represents *F* and *g* and *h*, and that bundle is a cauline bundle.

When the physiological grip of the condition of being 'minus' is strongest, the complete absence of internode enters into the stem and the occurrence of paired leaves is liable to be accompanied by the presence of approximated leaves at the interval appropriate for the divergence—i.e. at the third node above or below in the case of this individual plant of *D. opposita*.

Bulbils harvested from the plant which provided the material for Fig. 33, did not give in the next year any very closely approximated leaves, i.e. did not expose inheritance.

§19. *Phyllotactic pattern no. 2, being the first complicated by staging*

Staged foliage is found in the section Stenophora and, less marked, in some other sections. If staging be secondary as appears likely, the section Stenophora in which it most occurs being relatively primitive, it is desirable to investigate the staging and to do that with, in mind, the allied genera of Liliaceae—*Lilium*, *Polygoatum* and *Fritillaria*. Staging must have been reached in all of them from a spiral condition and it may be accompanied by an upsetting of the orderliness that is of not a little interest in regard to apical growth. The disorder in *Lilium* has attracted several botanists and puzzled them (see, for instance, the writings of Schoute in *Rec. Trav. bot. Neërland.* **11**, 94, 1922, and Plantefol in *Ann. Sci. Nat. Bot.* **11**, 198, 1948).

The long internode with which the stem of a Stenophora and that with which various species of *Lilium* hold up their first bunch of leaves are exactly alike in being strictly a single internode; but in *Tamus*, though the chief part of the growth made in the Spring Push is of one internode, the Push covers more than one internode. The intention is to get the first assimilating leaves above competing vegetation. In some species of *Lilium* a second elongated internode raises the flowers above the staged leaves. Questions arise on the relationship of these elongations to the plus elongations of my first phyllotactic pattern (p. 363).

Fig. 35 shows the way in which the staged leaves in *D. glauca* may stand in relation to each other. Components A and B show four leaves almost exactly at the same horizon but, as B shows, not spaced evenly. Close examination of the stem showed that there was one leaf, obviously the last of the four, squeezed, as the last comer, between the first and another. Interpreted on the supposition that the stem had plus and minus sides, one parastichy only appeared plus and the rest minus and there were three suppressed internodes. Component C, like the last, had four leaves approximated but not on a demonstrably genetic spiral. D and E are from a third plant, seen from its two sides: leaf no. 1 was the first of the group; it was followed by equally placed leaves on either side; and the group ended with leaf no. 4. Component F had four leaves suggesting a genetic spiral in the wrong direction. Component G had 5 leaves and again in disorder. That in the sequence there is disorder is obvious and the simplest explanation of it is that sliding growth at the previsual stage of emergence production displaces the emergences. We are not, however, much wiser by the explanation, for the question then becomes, what leads to the sliding growth? I refer the reader to Fig. 21 where the stoutness of a new stem still within the perennial bud shows the possibility of unequal lateral growth.

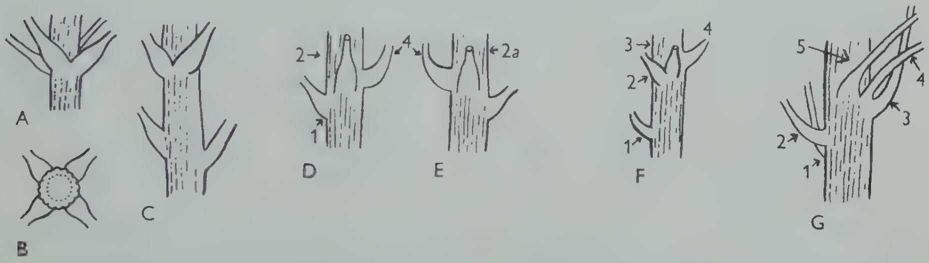

Fig. 35. Leaf-bases in *Dioscorea glauca* at the first stage of the leaves: A and B, a group of four leaves all at the one horizon but not equidistant around the stem; A, from the side; B, as seen from below; C, a group of four leaves dispersed in pairs; D and E, a group of four leaves arranged in a spiral in the first (D) which is to the right, but in the second (E) to the left; F, a group of four leaves arranged in a spiral to the right; G, a group of five leaves, the first two leaves in a spiral to the right but the other three in a spiral to the left.

In Fig. 21, component 4, a vertical section through the developing axis of *D. nipponica* shows very crowded leaves on a thickened axis; and the developing axis of *D. glauca* has likewise crowded leaves. Component C of Fig. 35 suggests that perhaps plus and minus sides are so strongly differentiated that in post-formational growth the narrow differences of horizon such as are seen in Fig. 21 D can be wiped out and even reversed during secondary extension. I have not been able to undertake the tedious investigations needed to prove this; but the idea is worth entertaining. Fig. 21 D shows that the plastochrone cannot be ignored. Assuming growth to maintain a constant rate, but the plastochrone to alter, the excessive length of the lowest internode might be partly delayed in continuing the output of further emergences. A new attempt to interpret the stem of *Lilium* might considerably aid in the understanding of the *Dioscorea*. Whatever the results, it is of some phylogenetic importance that the Dioscoreaceae and Liliaceae exhibit alike staged foliage.

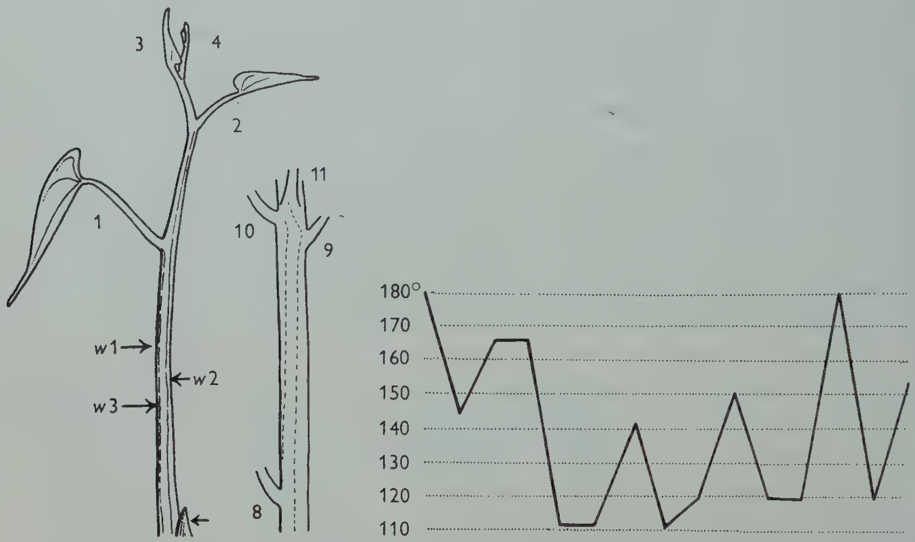

Fig. 36. A new stem of *Dioscorea alata* raised from a bulbil and now at its fourth leaf after the basal bract: *w* 1, *w* 2 and *w* 3 the wings over the mid-common bundles of three of the leaves, × ¼. B, The stem later, with the bases of its 8th to 11th leaves, the last three more or less staged, × ½. C, Graph of the angles of divergence of the stem up to its 15th leaf, during the establishment of which distichy was displaced by tristichy and this led into tetrastichy in the form of decussation in which the angle of 180° appears first in one of the two genetic spirals and then in the other.

§20. *Phyllotactic pattern, no.* 3—*the decussation of* Dioscorea alata *and its allies*

A decussate arrangement of leaves is obviously something that has entered late into the family. It is found only in species of relatively ample growth and appears on their stems as they approach their maximum circumference. It is most perfected in *D. alata* where it has pushed aside the pattern prevailing in the family.

For investigating it recourse was had to the bulbils of *D. alata*, their lesser growth promising quicker results than tubers; and they were germinated.

Fig. 37 is through the successive internodes of a stem; the numbers on the components are those of the leaf immediately above the internode holding the bundles. In the first component the whole leaf-trace from the first node is associated with four bundles of the second leaf and 1 of the third. The reader will observe gradual increase, internode by internode: in this particular stem the increase was as follows: 10, 11, 11, 13, 13, 13, then a leaf at the same horizon, 12, 12, 12, then a leaf at the same horizon, 12, and another leaf at the same horizon, 14, and a fourth leaf at the same horizon. The mid-common of leaf no. 2 is seen in the first component at an angle (calculated on the positions of the bundles) of 4 units out of 10 or 144°. Successively the angles calculated in this way followed as 164, 164, 111, 111, 138, 111, 120, 150, 120, 120, 180, 120, 153. These figures are made into a diagram in Fig. 36. The reader's attention is drawn to the evidence in the diagram of Fig. 36 that every third divergence is large which means every third parastichy is a plus parastichy as in Fig. 33 of *D. opposita*. To attain decussation out of this, as the last component of Fig. 38 indicates, two parastichies have to be plus parastichies. The stem attained it, but clearly not smoothly: when it was of sufficient circumference to accommodate leaves nos. 6 and 7 at the same horizon, it fell back until the course of the tristichous genetic spiral had reached again the side of the parastichy of leaf no. 6 and that brought a new opportunity of jumping from tristichy to tetrastichy which the previous failure shows to be an irregularity of a little difficulty.

To attain decussation meant that two emergences out of every four should be on plus parastichies and two on minus parastichies as exposed in the last component of Fig. 37; but that the plus and minus might come to the one horizon required a change in the sequence: it could not be plus-plus-minus-minus, but had to be plus-minus-plus-minus. The disturbances seen in *D. glauca* (Fig. 35) suggest that staging, confused with the plagiotropism of having plus and minus sides, can bring forward an emergence so early as to alter the succession in the previsual phase of the apex or so early that as yet it has not been observed.

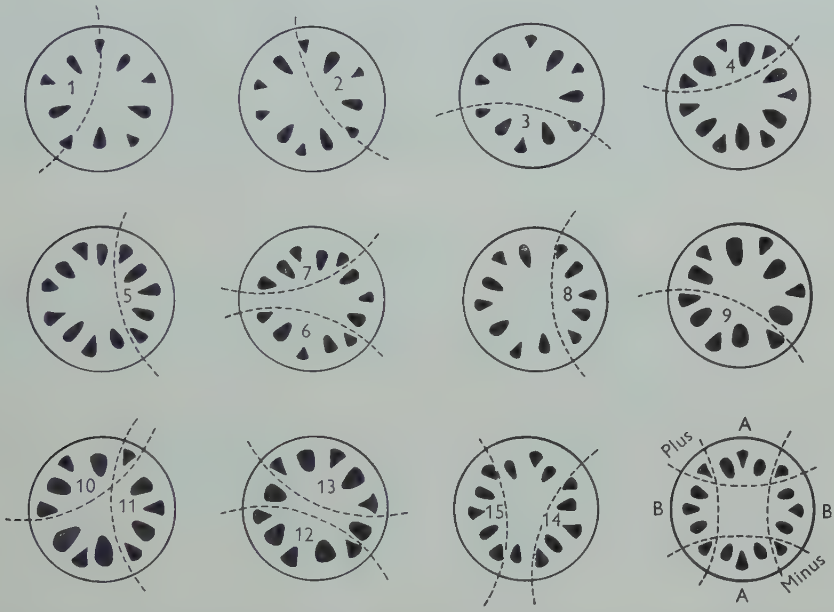

Fig. 37. The phyllotactic pattern at the base of the stem of *D. alata* up to the entry of decussation. Explanation in the text. The pattern varies from stem to stem, sometimes decussation entering more rapidly or sometimes more tardily. At leaves 9, 10 and 11 there is a tendency towards staging.

As soon as this has been brought about two genetic spirals may be postulated; they duplicate one another and the plastochrones for each are co-ordinated.

Decussation is a very stable pattern and evidently advantageous. It systematizes the vascular mesh at 16 bundles whereof every lateral common bundle travels down through no more internodes than one, every mid-common through two internodes and every cauline bundle through two internodes before it is extinguished. By contrast the five bundles of a leaf trace in a spiral stem of 16 bundles would need to travel through 4, 3, 3, 3, and 3 internodes, total 16 against 10. I have suggested that decussation has been a character added late among those of *Dioscorea* because it affects only a limited number of species; and this view is strengthened when we detect how it may be advantageous, and see how tenacious it is of its place when once gained.

Before passing on, it is convenient to record what I have ascertained regarding an aberrant clone of *D. alata* which confuses a fixed tristichy with its decussation. Kew received this clone in 1937 from the Director of Agriculture, British Guiana, as a wild food plant of the colony, and grew it, but its receipt was at an inconvenient season and it was lost but not until I had been puzzled by its alternate leaves. It reached Kew again, this time from Mozambique, and, grown in a pot in a glasshouse, it produced over several years shoots with alternate leaves; then planted in deep earth and allowed plenty of space a branch with the typical decussate foliage of *D. alata* was given off along with others with alternate leaves. Now I was able to name it with certainty. In the next year the same breaking back to type was repeated. It would now carry a stem of great length with decussate leaves from end to end as a branch from one with alternate leaves, tristichous without a break. In the latter the vascular bundles were fewer than 16 and it would seem that the jump to 16 had failed from inadequate expansion of the apex.

The clone was called 'jiba' by Mrs Faulkner who found it in Mozambique. It had perhaps been carried thither and also to the West Indies by Portuguese sailing ships in the sixteenth century; but I do not know whence they obtained it.

It seems to have become well spread wild in the islands of Trinidad and Tobago, whence the herbarium at Kew holds several sheets. So far these phyllotactic alterations seem to be by an upset behind the very apex, but perhaps following too closely for separate recognition. The suppression of emergences described in the earlier paper on the stems of *Tamus* suggests that they may occur so early as to leave no trace. The mathematically minded among botanists who seek precision at the apex may give a little attention to this.

§21. *The Dioscoreaceous leaf*

The typical leaf is simple and is so characteristic that it demonstrably underwent rigorous pressure in its early evolution. It is unmistakable. The compound leaf which is met with in a small number of the family's sections (see p. 379) is clearly an evolution from the simple leaf and it is convenient to concentrate in the first place on the simple leaf, with the compound to follow.

A family character of importance is that so much of the foliage is what Goebel called heteroblastic. In proposing that term he made a very useful distinction between heterophylly and heteroblasty: heterophylly is when two forms of leaves are produced, each to serve divergently a purpose for which it is designed: heteroblasty occurs when strength for growth fails, leaving the leaf unfinished according to the measure of its failure: the development has only one aim, but fails in varying degree to attain it. Inevitably the largest leaves for this reason are those that are proper for the definition of species; and unfortunately much indifferent work has been done by describers of species ignoring the fact that their characters ought to be taken from leaves of low positions on the stems.

The typical leaf has: (i) a long petiole with a pulvinus at each end; (ii) a broad lamina with arcuate primary nerves of which three only, whether the number be three or whether it be more than three, reach the apex of the leaf; (iii) there is a water-pore or water-pores on a projecting tip—a tip which is fully developed before the rest of the lamina is, and ceases growth, dying also, before the rest of the leaf; further (iv) the nervation between the primary nerves is reticulate.

The conspicuousness and early maturity of the glandular termination caused Cruger in 1882 to give to it the descriptive name of fore-runner tip.

All the four characters just enumerated are adaptations brought into service to make twining a success. They were not demanded before the introduction of twining, but would be such as the proto-Dioscoreaceae in their time brought forward. Petioles there certainly were, yet earlier, but not long petioles.

The reader is referred to the left-hand component of Fig. 38 which represents a lamina of *D. bulbifera* drawn over a circle of exactly the same superficies. The lamina shows the characteristic three primaries that reach the fore-runner tip and three pairs of accessory primaries which do not. The two parts of the lamina marked B and B_2 which extend beyond the circle are exactly compensated as to surface by A, A_2 and A_3 and in this way the strain on the petiole from the projection of the lamina is reduced. I calculate that if the lamina were of uniform material throughout, the strain would be reduced by the difference between the centre of the circle and letter G; but actually the reduction is much more, for the lamina is thickest at the base and is thin distally. This illustrates the meaning of auricles. They are a consequence of an endeavour to bring together the centre of gravity and the point where the strain is felt: and the picture of the evolution that one gets is of a lamina feathered with nerves from the petiole, which nerves were progressively drawn to a pulvinus that crept deeper and deeper into the base of the leaf. The perfecting of the pulvinus took the lead: it brought about the close approximation of the primaries, but the need of a long petiole was behind this.

The primaries are the longitudinal nerves of a Monocotyledon forced into arcuation by the way in which the broadening growth proceeds. They are orthotropic, and the first formed are able to retain their straightness against weaker and later primaries. Some of the divergence at the very base results from the crowding at the pulvinus where the outer have to yield to pressure from the inner.

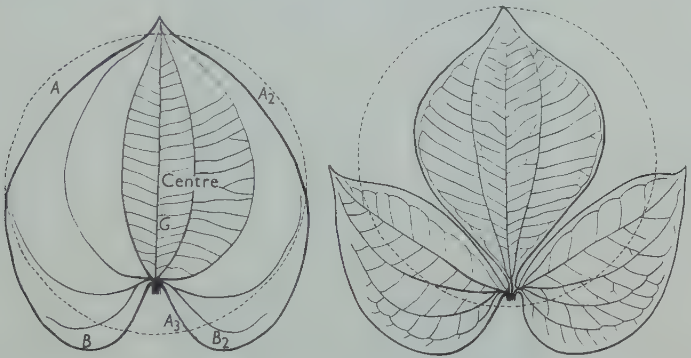

Fig. 38. A, The lamina of *Dioscorea bulbifera*, and *B*, the compound leaf of *D. dumetorum*, each over a circle of the same superficies. Explanation in the text.

The secondary nerves are more conspicuous in *D. bulbifera* than is usual in *Dioscorea*; they run with a ladder-like precision between the primaries and, because they are fixed at both ends, are pulled taut as the primaries become arcuate. The nerves and nervules which appear later may be divided into the bound and free-ended. Those bound are subjected to pulls which make their courses angular.

Fig. 39 illustrates the structure of the network. Each new and pliant nervule seeks union with another; but the other must be plastic if it is to be receptive; if its growth has gone too far the union cannot take place. A line drawn down the figure between the two 0's of the scales crosses 14 nerves or nervules; a line at the distance of 2 mm. from the midrib (which is the nerve on the left) crosses half as many again; and so also all other parallel lines; but a line from 0 in the lower scale following the lateral primary towards 12 in the upper scale crosses a reduced number. There is this similarity between one of these least nervules and the midrib that they find no nerve ready to relieve their discharge; but the midrib discharges by the terminal water-gland. There is this contrasting difference between them, that the midrib is straight and strong, but the nervules are curled from being weak.

Experimental mutilation of the leaves readily proves that the midrib's straightness is maintained by orthotropy (see, for instance, a paper entitled 'On the growth and tensions between the nerves of the leaf-blade of *Tamus*' (*J. Bot.* 1939, p. 330)) and that orthotropy, weaker as they are later, is in all the other primaries; and that they retain their orthotropy, though masked in the plane of the leaf, when arcuation is able to overcome it.

The first laterals grow longer than the midrib and push against one another; let one be cut and the push of the other bends the midrib. Leaves can readily be found in the hedgerows where marginal damage by snails leads to such distortion; and it is easy to imitate them.

The secondary nerves show orthotropy (Fig. 38) in their pulls on each other, and the ladder that they form in *D. bulbifera* shows it well.

In the matter of poising the leaf, the lamina is master of the petiole in all parts, for the shaft does not grow if the lamina be removed; it even dies. This mastery is illustrated in another paper (*Proc. Linn. Soc.*, **155**, 252, 1944) seeking to explain how the stimulation by light is summed for the whole lamina, whereupon the upper pulvinus, responding, lifts or lowers the tip by means of the hinge and at the same time calls out a horizontal movement which directs the apex to the right or the left as may be to advantage; tattered laminae get new positions as shown in that paper (p. 268). The lower pulvinus assists, for co-operation is required between the two to command every possible position.

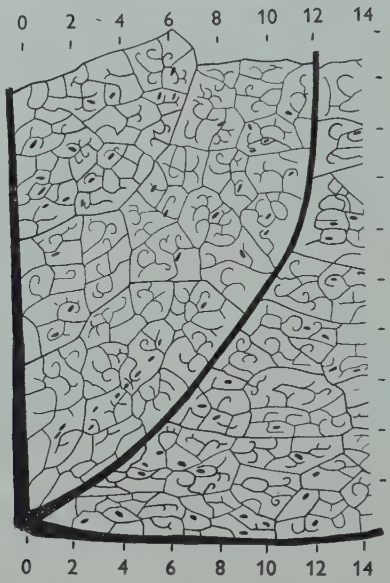

Fig. 39. Three square centimetres from a young leaf of *Tamus communis* showing the nervation in detail and the position and angle of the raphides. The scale above and below is in millimetres. Explanation in the text.

Several botanists, notably Schenck (*Beih. Biol. Anat. Lianen*, 1880), have written of the connexion between a climbing habit and a broad lamina such as we find in the Dioscoreaceae. The most intimately related families of the Liliales contribute illustrations, for a broad lamina is seen in these climbers—*Smilax*, *Eustrephus*, *Geitonoplesium*, *Lapageria*, *Bomarea* and *Stemona*. These, all clamberers, point to the interlocking of climbing with a broad lamina; twining is not only interlocked with a broad lamina but also with a long petiole, for a twiner grows upwards under the foliage of its victim and uses its petiole for thrusting its own leaves, if it can, beyond the victim's leaves. In this way twining is a refinement of climbing: it forces the stems to be unencumbered, demands in the case of Dioscoreaceae that they be produced with the maximum economy and the maximum speed and they are therefore slender. To match the slenderness against a disproportionate largeness of lamina, a call for water from down the stem at a distance has had to be met by special developments. The large water-pore at the leaf-tip serves to steady the current. Travellers in the humid tropics see and record the resultant drops of water hanging on the leaf-tip when the air of dawn is saturated. Though the apex looks like a drip-tip and serves as one during tropical rain-storms, its shape is probably attributable entirely to the need of setting aside at a very early date enough of the leaf to carry the gland; and so is another consequence of the twining habit.

Now it is time to refer to the compound leaf which is drawn in Fig. 38 over a circle of the same superficies as its three leaflets taken together. The reader will note that the terminal leaflet carries the gland at which meet the three primary nerves which characterize the family, and that the lateral leaflets carry the auricles. On this evidence it is reasonable to hold that the compound leaf was derived, wherever it appears, from the simple after the family had established itself as a family of twiners. Further information on compound leaves is deferred to p. 379.

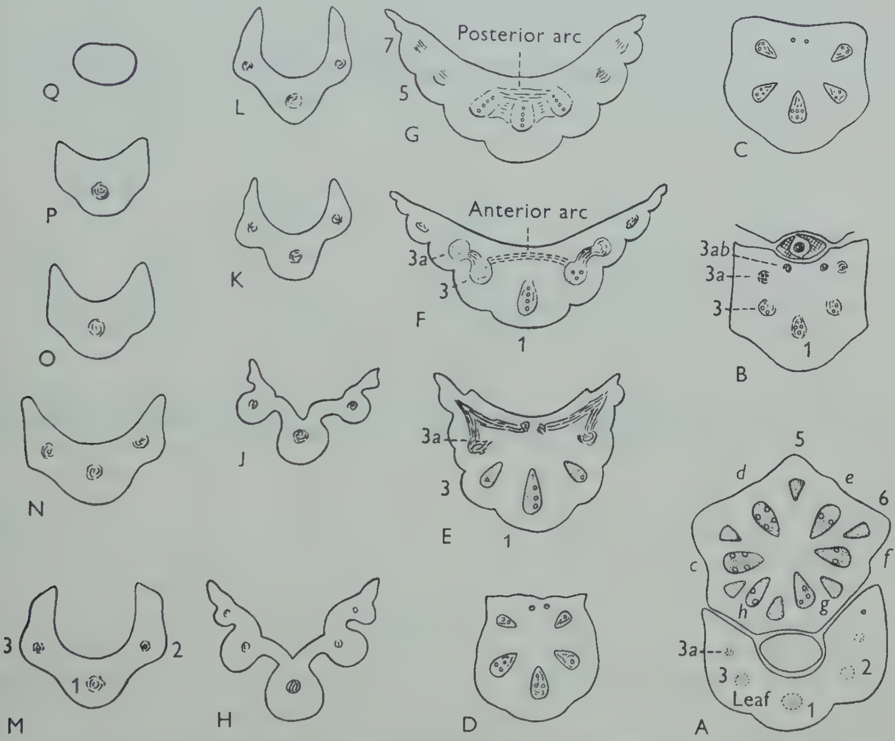

Fig. 40. Transverse sections through a young leaf of *Dioscorea bulbifera*, microtomed, reading from the end backwards: A, just separated from the stem; 1, 2 and 3, the three common bundles, 3*a* the first branch of bundle 3 the course of which as also of the branch of 3*a* up to the upper pulvinus are indicated in components B, C and D. Components D and E through the forming upper pulvinus showing the anterior vascular arc forming and the commencement of the first of the outer primary bundles appearing while the inverted bundles disappear. Component G the posterior vascular arc completed. H and J the lamina are surrounded by parenchymatous growth and the tissue between them by its own growth is billowed upwards. K to Q there is no billowing of parenchyma, but a gradual flattening to the apex.

A terminal vegetative bud of *D. bulbifera*, microtomed into a little short of 1000 sec- ions, furnished the material for Fig. 40. Component A of the figure is a section showing he relation of the base of the petiole to the parent stem; it passes through the axil above he lower pulvinus and above the commissure which gives communication between the hree common nerves entering the leaf. The reader will find the lettering on it in agree- nent with the lettering on the earlier Fig. 31 (p. 362). Below the horizon of this section the outer of the bundles had branched and the branch was to branch again, so that the bundles in the petiole had been increased to 5 and would be increased to 7, after which all run unbroken through the shaft to the upper pulvinus, the lateral, which are the smallest, edging round the shaft of the petiole until the seven are in a ring like the bundles of a stem with the protoxylem inwards. The upper pulvinus receives them and connects them together by a commissure[1] wherein the small bundles are lost (see component E). Component B shows the angles of the embracing base of the petiole disappearing, and component C that they are much diminished in the shaft, but that, as component D shows, they gain strength as the upper pulvinus is approached.

The service that the pulvinus does as a hinge demands that it should be flat. Changes of positions of parts producing this flatness follow one another closely; components E, F and G represent them; they are compressed into 1/100 of the length that the leaf had attained. The petiole made one-tenth only at the time and nine-tenths were above the horizon of the components E, F and G.

The components from G forward show that the distal end of the growing leaf can be regarded as of two parts, one folded towards the stem into a V, the other into an U. In the part folded into a V the primaries have appeared like wicks in candles and are lightly linked together by tissue which will receive the web. The parenchyma of the 'candles' appears as a ready water store. The midrib is now acquiring orthotropism. Growth at the apex in the tissue into which the midrib runs is slackening around the glandular end and as that happens the terminal parts of the three primaries become tied together whereby the shape of the fore-runner tip is fixed. It will be noticed that the web of tissue joining bundle to bundle is full and by its position in regard to the primaries it is billowed upwards, having made growth enough for the primaries to be in no way dragged by it. The V-angle takes its shape from the position it has towards the upper side of the bundle. The angle, whether V or U, helps the lamina to retain touch with the stem which is to the good of both for the faces in contact give protection to each other and they share the mucilage of whatever colleters there may be. The growth at this time is more in elongation than in broadening; later a very easily identifiable basipetal wave will increase the rate of broadening beyond the rate of elongation.

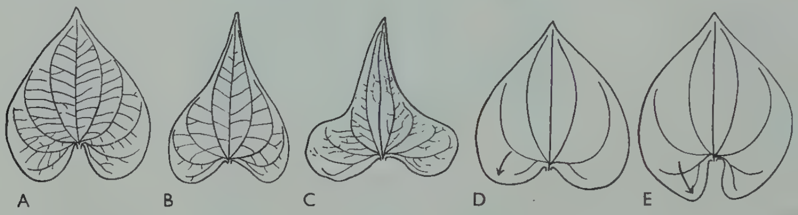

Fig. 41. The lamina of *Tamus communis*. A, Typical in outline; B, when the strength of the basipetal wave of growth is deficient early; C, when after deficiency it becomes considerably reinforced; D, the normal effect of the baffle at the base; E, the basipetal wave sweeps round the baffle.

I refer the reader again to Fig. 38, that I may remind him by how much the first lateral primary has become longer than the midrib when their growth is done and how this greater length is accommodated by curvature. The midrib ceases its elongation from both ends. There are two factors in this: one is that the basal part of the leaf is thickened and hardening; the other is that the basipetal wave of growth passes away from the base of the fore-runner tip and the slack in its wake fixes the parts as it passes from them. Commencing unavoidably with the midrib, and overtaking the lateral primaries in turn, it ties them in position through the nervules into which they have broken up.

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[1] The commissure—Queva's 'anterior arc', is part of a complete ring; but in *Trichopus* the ring is broken in this, the anterior part (see Watson in *Notes Roy. Bot. Gard. Edinb.* **19**, 149, 1936).

When the basipetal wave approaches the base of the lamina, the already somewhat resistant area near the pulvinus acts as a baffle which splits the wave to expend itself in the auricles. The auricles depend therefore for size on the strength that is left in the wave; and on its continuance depends the narrowness of the sinus about the petiole. Fig. 42 is inserted to illustrate this; it gives the outlines of leaves of *D. alata* showing that growth which is vigorous enough to cause the first accessory primary to run at an angle from the midrib wider than 90° is an accompaniment of a large auricle. The leaves used were selected for their size from plants cultivated in the Botanic Gardens, Singapore, in a study of the clones collected from many parts of the tropics.

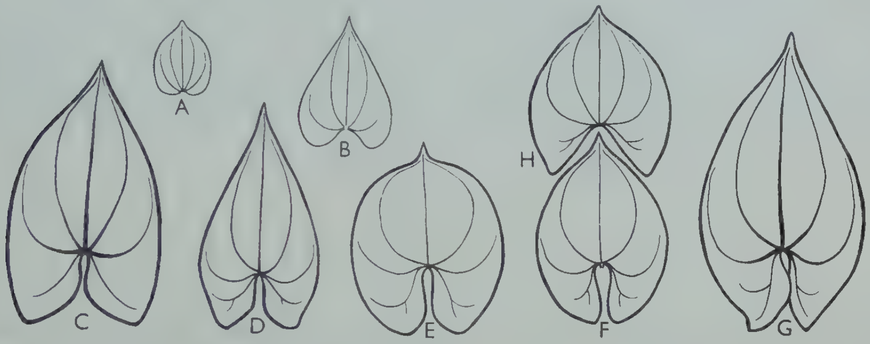

Fig. 42. Laminae of *D. alata*. A, from the flowering part of the plant showing that power to grow fails before the first accessory primary is driven towards a right angle with the midrib and therefore there can be no auricle; B, from among the leaves normal over the purely assimilating part of the stem; the waves of growth produce cordation; C, D, E, F and G, the largest laminae produced by cultivated and well-manured plants in which the auricles were stimulated to their maximum; in all the first accessory nerve had been carried a little beyond the right angle and the auricle had been greatly extended parallel (in the dried state) to the petiole; H, a state which sometimes appears and awaits experimental investigation. All ×$\frac{1}{7}$.

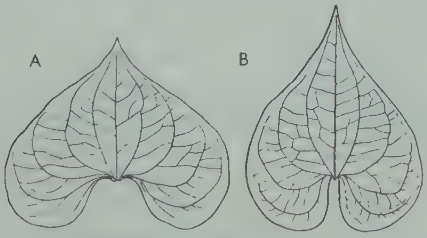

Fig. 43. Leaves of *Tamus communis* from two neighbouring plants of the same hedgerow, the one extremely broad; the surface of the two equal; midrib in length respectively 7 and 9·5 cm.; breadth 12 and 9·5 cm.

The diverging of the primary nerves provides the foundation and is at the beginning of the building up. In *D. bulbifera* the nerves are more in number than in most species; and in agreement with that the margin of the leaf is made to sweep round widely; they are put in place in turn. Here and there in the very wide distributional area over which this species is spread, there are dispersed in a population with laminae shaped as in Fig. 38, individuals with narrower leaves: these as seen in and near the island of Penang have been assigned to the var. *heterophylla* (Roxb.) and as seen in the Sikkim Himalaya to the var. *simba*. It is obvious that the varieties get their narrowed laminae from weakness in an outward wave of growth that comes into being before the basipetal wave exercises its full influence; it may be the end of general enlargement.

These two varieties of *D. bulbifera* have received varietal names, not because their heredity has been tested, but because by their local frequency the character must be inherited. In contrast in *Tamus* parallel differences (as in Fig. 43) do not need varietal distinction because the broad and unusual one is not known to have any geographical abundance.

In broad leaves the outermost primary is late enough in forming to have no direct connexion with the pulvinus but has union with that which immediately preceded it. The baffle has intervened.

The process of broadening during growth enters after elongation and in rate overtakes elongation as Fig. 44 shows. For the making of this figure a large number of actively growing stems were taken and the breadth and length of all the leaves measured. Then all the youngest were eliminated by taking the stage on the left side of the figure as one limit and the data for the preceding ten leaves gave the graph. The rate of broadening is seen to overtake and to pass the rate of elongating. The angle to the midrib that the raphides take, as seen in Fig. 39, can be used to show that it is not broadening of cells but rotation about the pulvinus that accounts for the overtaking. The reader is referred to the *J. Bot.* (1940, p. 7) for an exact representation of the positions of raphides in leaves of *Tamus*. Their orientation is directed by the arcuation of the primaries. The next paragraph accounts for sinuation in the margin.

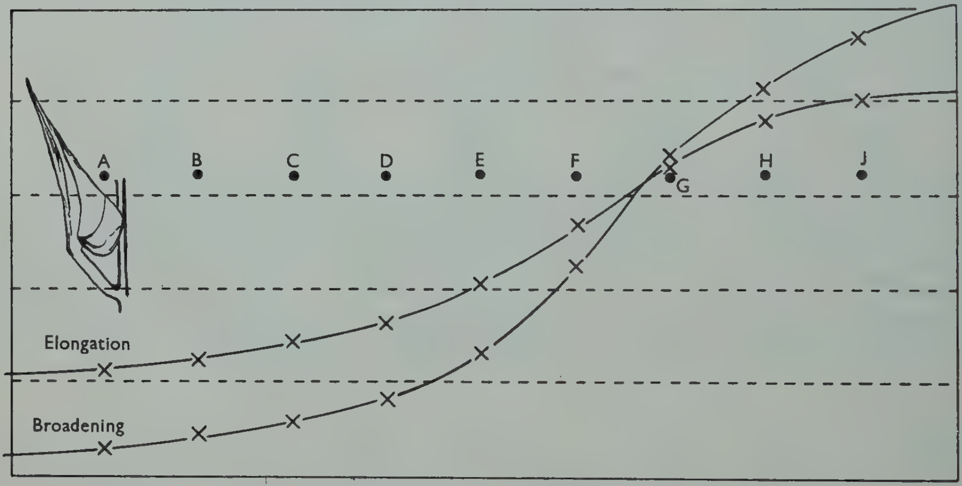

Fig. 44. Graph of the relation between elongation and broadening in the expanding leaves of *T. communis*, being the average increase of the ten leaves whose growth has passed beyond the condition of the young leaf at A.

On an actively growing stem there is undoubtedly a keen competition between neighbouring leaves for materials for growth. In *T. communis*, if the materials allow, a lamina of the shape of component A of Fig. 41 results; but the competition very generally results in the shape of component B as is easy to prove by such experimental decapitation as results in the uppermost of the leaves left receiving food and water which would have passed beyond it. By this the shape of component A can be secured and is produced. Thus it is that the sinuation so common in that plant and the cause of Linnaeus making a species *T. cretica* can be an accident. As with *Tamus* so with other species of *Dioscorea*; but the fewer the primary nerves the more susceptible.

It is of course the case that a sinuation which may appear from maladjustment may become a fixed character of general or partial reappearance as in the section Rhacodophyllum (see p. 378 onwards).

We reach here an exceedingly interesting fact, namely though the laminae of the seedling leaves be small the lamina is fully formed and properly auriculate. This is achieved by the way in which the seedling limits the number of leaves that it produces. When the seed germinates a single assimilating leaf is sent into the air; and though a reserve be present in support, it is not allowed to grow. That single leaf gets all the available nourishment; and growth as to shape runs the full course, and even overruns the full course. In *Tamus*, for instance, the first assimilating leaf is broader than the typical leaf as if the strengthening of the seedling contributed an excess in nourishment (see for a figure of it, *J. Bot.* 1945, p. 18) A further illustration may be obtained from *D. laurifolia*, in which the first assimilating leaf is abundantly auricled, but most of the leaves on the stems are reduced by heteroblasty (see *Flora Malesiana* (1), **4/3**, 323). There is no heterophylly here, but the leaves are of three kinds: (i) undersized as the plant has not yet strengthened; (ii) typical; and (iii) underdeveloped or heteroblastic.

An observation which remains isolated is that the reduction in size of the first assimilating leaf of *D. pyrenaica*, while unaccompanied by alteration in the shape of the auricles, is accompanied by a failure of the lateral primaries to reach the apex.

§22. *The measure in which Dioscoreaceae approach megaphylly*

When the proto-Dioscoreaceae were emergent from the proto-Liliaceae as twiners commencing anew each year their effort to reach the light, enlargement of the lamina of the leaf would seem to have been advantageous and to have met with the response that has tended to shape the leaves of climbing plants in general, but the increase in weight and the expenditure of material was a tax on the plant in a hurry and faced with the intensifying of competition as the supporting trees spread their leaves, the expenditure on lower leaves possibly soon became unremunerative. The compromise may be roughly the superficies for a full grown leaf to be 50–75 cm.^{2} and for a large leaf 100 cm.^{2}.

This is very far from the megaphylly which characterizes the Palmae, Musaceae, Zingiberaceae, Cannaceae, and Araceae. These produce their large leaves under forest cover and hold them long. Dioscoreaceae are remote from their megaphylly.

Our native *Tamus communis* on germination produces a first assimilating leaf of 2–2·5 cm.^{2} and year by year the earliest of each new growth increases in size to about 75 cm.^{2}. In the humid tropics Dioscoreas grow a little larger.

Hansgirg classified the leaves as 'wind leaves' (*Phyllobiologie*, p. 131, 1903), meaning resistant to wind. This they seem invariably to be: the arcuation of the nerves strengthening the lamina near the margin, and the position in which the lamina is held shoots off the water of a tropical rainstorm by the drip tip.

These are my measurements in which the superficies exceeded 200 cm.^{2}. All the measurements are in square centimetres. I would count the records 645 for *D. alata* and 238 for *Tamus* as abnormalities, the others as the limits of normality. *Dioscorea sansibarensis* 1277, 1207 and 1020; the three largest leaves of a plant cultivated at Kew. *D. bulbifera* 807 from Negri Sembilan in Malaya; 806 from the Hawaiian islands; 745 from Upper Perak in Malaya; 368 from the Sikkim Himalaya; 346 from Malaya. *D. alata* 645; from Penang, a clone called 'ubi atas' or top-side tubers from its numerous bulbils; 235 from cultivation at Kew; 206 from cultivation in Singapore. *D. preussii* 504; from the Oya province of Nigeria. *D. puber* 492 from Chittagong; 292 from Java. *D. trifida* 383 from cultivation in Trinidad. *D. piscatorum* 320; from British North Borneo. *D. flabellifolia* 301; from the Philippine islands. *D. polyclades* 292 and 285; from Malaya. *D. pyrifolia* 284 and 211; from Malaya. *Stenomeris dioscoreifolia* 283; from Luzon, Philippine islands. *Dioscorea esculenta* 272; from Luzon, Philippine islands. *D. ledermannii* 252; from the Palao islands. *Tamus communis* 238; from Surrey, Britain. *Dioscorea schimperiana* 234; from Northern Nigeria. *D. abyssinica* 229; from Uganda.

All the above were simple leaves. Species with compound leaves may reach a greater surface, if the leaflets be taken together; thus a trifoliate leaf of *D. dumetorum* attained 1520 cm.^{2} and that of *D. hispida* Dennst. from the south of the Philippine islands 996 cm.^{2}. A still larger leaf was obtained from a plant of *D. cochleari-apiculata* in the southern part of Tanganyika—the three leaflets together just over 1900 cm.^{2}. In general, the compounding of the leaves favours an increase of surface to each position of leaf-carrying on the stem. We find that compounding of leaves had recurred in the evolution of the family as if there is gain in it. To this I return on p. 379.

§23. *The phyllode theory*

The phyllode theory seeks to explain the origin of certain peculiar structures terminating the leaves of various Monocotyledons—the fore-runner tip for instance—by calling them the lamina and calling the functional lamina a petiole. It is a theory which, when applied to *Dioscorea*, would attribute to them an astonishing double petiole. The alternative and obviously satisfying belief is that the fore-runner tip is an apical gland. In several papers and in her book—*Monocotyledons*—Dr Arber has called attention to the solid apex terminating the leaf of various species of Liliaceae. In *J. Linn. Soc.* (*Bot.*), **45**, 417, 1933) without mention of the Dioscoreaceae, she included with the others the solid apex of *Smilax*, interpreting it as an unextended petiolar organ. Though I am not producing any facts drawn from *Smilax*, it is not possible to avoid feeling that what is the case in *Smilax* is the case in *Dioscorea*: but agreeing with Campbell (*Ann. Bot.* **44**, 319, 1939) that the phyllode theory cannot be applied to the Dioscoreaceae, the conclusion is that it applies to neither.

The presence of an apical gland is the primary fact; not the shape of the end that carries it. The fore-runner tip is indeed conspicuous in many species of the Dioscoreaceae, e.g. *D. bulbifera* (Fig. 38) and *D. alata* (Fig. 42); but in most of the species it is only a mucro and in the seedling leaf of *D. pyrenaica* the gland is flush with the surface. The gland functions when the dioscoreaceous leaf is young; when inactivity comes over it the projection which holds it becomes a drip-tip.

§24. *Stipules*

I have commented that the twining stem of the Dioscoreaceae should be without encumbrances. This is almost but not absolutely the case: it carries rarely and irregularly emergences where stem and leaf join which by their position fall within the accepted definition of stipules. Sinnott and Bailey have shown that the majority of angiospermous genera that possess emergences have three common bundles entering the leaf and that the stipules are extruded over the laterals of the three (*Amer. J. Bot.* **1**, 442, 1914). So it is in Dioscoreaceae: in which emergences may and very irregularly do appear over the lateral common bundles. They grow into different forms. They add to the assimilating surface in *D. bulbifera*; they add to the rigidity of the base of the petiole in *D. sansibarensis*; they mimic prickles in *Tamus communis* but are weak and ineffective as such. One may examine thousands of specimens of *D. bulbifera* without finding a stipulate leaf, and in like manner many specimens of *Tamus* without finding a pair of the weak prickles that it has. The broadening of the base of the petiole in *D. sansibarensis* is more constant in appearing: it appears on the lowest leaves which are below the horizon of twining where, indeed, the stems may be prevented from slipping downwards by coming in contact with support in a thicket, but that they so function has not been shown. As characters produced below the horizon of twining their production there does not belie the generalization that twining stems should be unencumbered. Sometimes the stems of *D. bulbifera* are more winged than is usual. The stipules when present arise over common bundles as the wings do; and occupation of the same position is interesting. Sometimes little stiplules occupy the same position in the abundantly winged *D. alata*.

The Madagascan *D. seriflora*, *D. comorensis*, of the Comoro Islands, *D. paleata*, of the Belgian Congo, also have stipules with a surface adequate to add to the assimilation. Such stipules seem to have no taxonomic value. The soft prickles, as in *Tamus*, reappear in several species of the section Stenophora, e.g. in *D. panthaica*, *D. biserialis*, *D. hypoglauca*, *D. chingii*, *D. tenuipes*, *D. tokoro*, *D. quinqueloba* and *D. membranacea*, always very sparingly. *D. birmanica*, a rather isolated species of the same section, has prickles abundantly in the same position. In the section Lasiophyton *D. kamoonensis* may have some soft prickles. It is noteworthy that strong rigid defensive prickles are absent from all these.

It is a safe generalization that stipules are assimilated to local demands; if protection be required to protecting; if assimilation to assimilating, but they have no real place in the life of the Dioscoreaceae, though at least in Stenophora they have some taxonomic value.

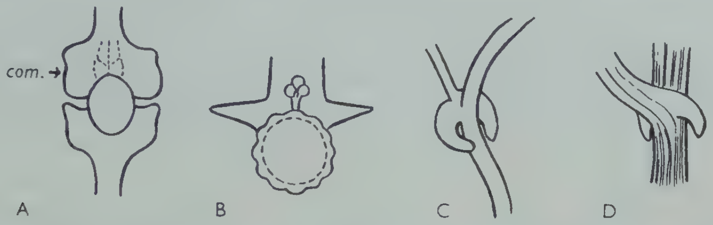

Fig. 45. Stipules. A. *D. sansibarensis*, nat. size. B, *Tamus communis* (Linn.), × 4; C, *D. paleata*, nat. size; D, *D. seriflora*, nat. size. The position of the vascular bundles is indicated in A, but they can only be seen on section.

§25. *Lobed leaves*

Lobing is a greater interference with the margin of the leaf than the sinuation described on p. 372, and is attributable to an interaction between the growth that starts parallel to the primary bundles and the later commencing basipetal wave: but, the urges lying deeper, and being repeated, it is probably beyond experimental examination by decapitating the extending stem. Fig. 46 illustrates lobed leaves. The basipetal wave passes downward from the distal parts of the accessory primaries without fixing the ends.

Lobing is found in the following sections: in Asia species of Stenophora (Fig. 42 J and M); in Africa in all the species of Rhacodophyllum (D, E, F, G, H) and in the only species of Macroura (C), then transitionally towards sinuation in Testudinaria (B); and in America in the section Stenocarpa.

Lobing characterizes the youth leaves of *D. sansibarensis* (C) and the following interesting observation, which came to me from Miss Marie Scott, shows how consistently it is produced. She told me that the University of Wisconsin had thought it well to keep the plant alive through the winter as a bulbil, and, in consequence of doing so, had not been getting the cordate entire foliage of vigorous plants, but only youth leaves. The other lobed leaves in the figure are not youth leaves, but leaves of mature form, and are to be found both large and small. It is interesting that *D. buchanani* of the same section has lobed leaves and leaves without lobes and that as in *D. sansibarensis* it is the largest that are without lobes.

Apparently it is easier to give origin to lobes if the primary nerves are well spaced than if they are close together, but there is no absolute rule; and the nerves are more numerous in the section Stenophora than in the others.

Blume's *D. repanda* (*Enum. Plant. Java*, **1**, 22) was not a good species, but a youth form. Botanists who tried to identify it have been at variance, their choice mostly a youth form of *D. pyrifolia*. Its outline may be reasonably attributed to weakness in the basipetal wave.

Goebel paid attention to youth forms (*Einleit. Morph. Pflanzen*), and attributed their formation to poor conditions such as deficient light or unsuitable temperatures. There is room for further study as Ashby hints (*New Phytol.* **47**, 153).

§26. *Short petioles*

A small number of species have short petioles and they are connected with absence of auricles. The most interesting of them is *D. hexagona*, which has been mentioned on p. 341 as a plant of the grassy savannahs of Madagascar. It stands strictly erect, no taller than the associated grasses; but, if it chances to be where the soil is good enough to support a bush, it profits by the increased moisture and shade to be just tall enough to twine with its stem tips. Its lanceolate laminae grow upwards on petioles 1–2 mm. long. In the thin forest beyond the edge of the savannah its close ally *D. soso* connects it with typical Dioscoreas. They belong to the section Brachyandra and so does another species, *D. heteropoda*. In similar savannahs of southern central Brazil *D. anomala* and *D. stenophylla*, of the section Dematostemon, grow in the same way and their short petioles and laminae narrowed into them are obvious adaptations to their habitat. The characters have entered by parallel evolution, and date the savannahs in either country as old enough for the evolution.

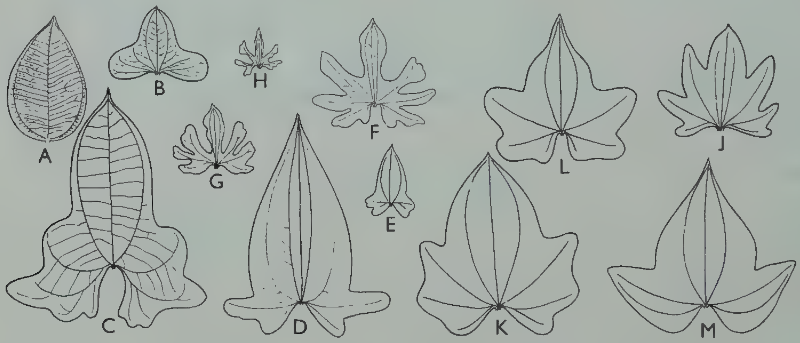

Fig. 46. Interplay of the accessory primary nerves and the basipetal wave of growth: laminae × $\frac{1}{7}$. A, of *D.* (*Enantiophyllum*) *smilacifolia* which has no accessory primaries; B, of *D.* (*Testudinaria*) *sylvatica* and M, of *D.* (*Stenophora*) *membranacea*, in which the wave strengthens towards its end; D and E, of *D.* (*Rhacodophyllum*) *rupicola* in which the wave comes near to anticipating the accessory primaries; J, K and L: J, of *D.* (*Rhacodophyllum*) *diversifolia*; K, of *D.* (*Stenophora*) *nipponica*, L, of *D.* (*Chirophyllum*) *bryoniifolia*, where the wave is rather late; and F, G and H, of *D.* (*Rhacodophyllum*) *undatiloba*, where it is very late. Lastly C is the youth leaf of *D.* (*Macroura*) *sansibarensis* in which the wave is much later than in the fully entire leaf carried by vigorous plants.

Short petioles, but not so short as those of the species already named, occur in the section Enantiophyllum in Malaysia and Indo-china. There are several in Malaysia, but *D. brevipetiolata* only in Indo-China. The laminae in them are usually rounded at the base, and it is clear that the basipetal wave of growth fades out early. Its arrest and that of the petiole may be described as interference with the upper pulvinus as its focus.

§27. *Pediments*

The subject of petioles that project the laminae forward, leads naturally to the subject of the pediment that thrusts the flower forward, though the ultimate purpose be quite unlike. Little pediments as brackets under the leaves (see p. 362) are more or less invariable in the family: the pediment that I deal with here replaces a pedicel as a support for the flower and is met with in various species of the section Lasiophyton—it is a pediment which does two services, for it carries out the protecting bract along with the flower. Its most conspicuous development is in the widespread African *D. quartiniana* and the Asiatic *D. kamoonensis*—species not very close to each other but alike in the pediment being 1–2 mm. long. There are several species with shorter pediments.

§28. *Compound leaves*

There are no species with compound leaves in the small or satellite genera of Dioscoreaceae, but five sections of *Dioscorea* have them: two are in Asia—Lasiophyton and Illigerastrum, one is in Africa—Lasiophyton, and a second Cardiocapsa, is in Madagascar; two as I place them—Stenocarpa and Trifoliatae, are in South America. Knuth has put four species with compound leaves into the section Apodostemon; but they are better placed in Trifoliatae. Trifoliatae and Stenocarpa excepted, the sections show no very intimate relationship to each other; and it would seem that compounding has appeared at least four times during the history of Dioscoreaceae.

Compounding breaks up the pulvinus so that it is no longer a simple hinge. The effect on its working is not evident; but it has not prevented some of the compound-leaved plants from obtaining wide dispersal. The largest of the sections in number of species and widest in distribution is Lasiophyton, with a spread from the Atlantic coast of Africa to the furthest parts of the Pacific; but Man may have been the agent in its spread in the Pacific. The reconstructed Trifoliatae has five to six species; the others fewer. The five sections are not alike in the direction of twining nor in the direction of the wing. Lasiophyton, Illigerastrum, Stenocarpa and Cardiocapsa twine to the left: Trifoliatae in reverse. Lasiophyton, Trifoliatae and Stenocarpa have seeds winged from the end; the others are winged all round.

Comment has been made (p. 375) that compounding may enable a larger assimilating surface to be exposed per axil; and if it be right that such little increases as wings on the stem are advantageous, so may compounding bring an advantage. A slight advantage may be obtained by independently adjusting the light-fixed poise of the leaflets and by their independent yielding to the fury of a tropical storm. Experiments are suggested.

The indication that compounding has happened in four lines is intriguing because the pulvinus appears to have been so important in shaping the family as to resist devolution. Compounding looks like exaggerated lobing, but that it is not. The lobing of Rhacodophyllum (for illustration see Fig. 46) is an end that could not lead to compounding. The way to compounding is to be sought in the development of the pulvinus. Could certain lines have so changed their habitats as to need the pulvinus less? The pulvinus may be partly altered. In fig. 47 A the inner three primaries meet in the fore-runner tip, but are fused at the base: in Fig. 47 B only one nerve reaches the fore-runner tip. Compounding and lobing come from operations in different fields; and it is this that seems to say that the first should not be regarded as an extension of the second. Compounding and lobing may occur together in the same leaf, as Fig. 47 C shows. Fig. 48 E makes them alternatives. The interesting passage of the basipetal wave of growth down such a leaf, as in Fig. 38 B with a leaping from terminal leaf to the lateral leaf shows the wave an independent factor; Fig. 48 A and B shows that a leaflet without the unbalance of an auricle can be produced.

Fig. 48 is devoted entirely to the shape of the leaves in the variable and widespread African *D. quartiniana*, because each of the forms drawn has been given a specific name, and this confusion cannot be left without correction. Undoubtedly the ancestral leaf of this species was trifoliolate with auricular enlargement on the outer side of the lateral leaflets (as Fig. 48 F). Figs. 48 C and D are what Fig. 48 F would give if heteroblastic; Fig. 48 A, H and J are extreme variants.

Lasiophyton is the only section which produces more than three leaflets: this it does in the African *D. quartiniana* and in eight Asiatic species. Of these *D. pentaphylla* is the most widespread in Asia; and all the other seven occur within the area of *D. pentaphylla*. *D. quartiniana* is widespread in Africa; and here again no species of the section spreads beyond *D. quartiniana*.

The compound leaved sections of the Old World are so divergent from all other sections that their immediate ancestry is not evident.

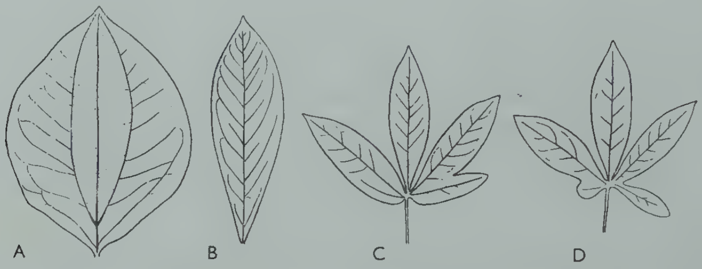

Fig. 47. Compound leaves, ×$\frac{1}{3}$. A, The terminal leaflet of *D. dumetorum* with the three primary nerves parting above the base; B, the terminal leaflet of *D. crotalariifolia* in which only one nerve reaches the apex; C and D, leaves of *D. crotalariifolia* showing lobing on the lateral leaflets.

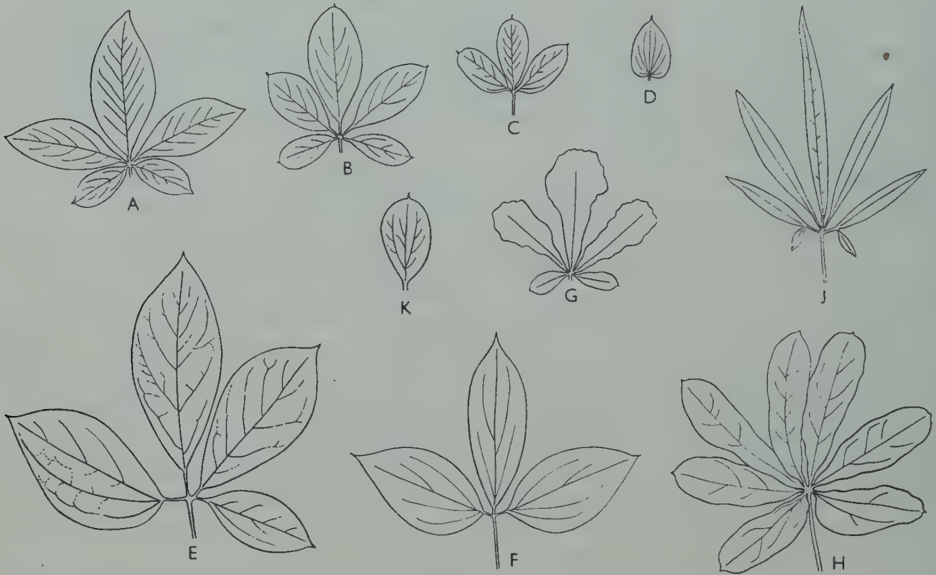

Fig. 48. The various forms that the leaf of *D. quartiniana* takes, ×$\frac{1}{3}$. A and B. The typical leaf which is 5-leaved and has all the leaflets penninerved; E, a leaflet equating an auricle to an outer leaflet; C, a trifoliate form on which *D. apiculata* was described; D, a heteroblastic leaf of the same form such as has received the name '*D. holstii*'; K, an abnormality which has received the name '*D. verdickii*'; G and H, the variety which is '*D. excisa*' (G does not retain evidence of the auricles except in that measure which A and B do, namely in the outer leaflets); J, a leaf of the variety *schleibenii*; F, presumed form of ancestral leaf.

§29. *Germination and leaf-suppression in the seedling*

The cotyledon does only two of the services that commonly fall to cotyledons; it adsorbs the food that the seed holds and it pushes the rest of the little plant out of the seed. The pushing must continue until the cauline apex is beyond the seed-coats and the petiole of the cotyledon too thick to pass out. Thereafter the cotyledon grows to the size of the cavity which its eats out for itself by draining the endosperm. Then it dies.

Its stalk usually elongates a little, but it may get length enough to permit a geotropic movement that puts the hypocotyl vertical in *D. pyrenaica*; on which the whole hypocotyl can become the initial tuber. It is otherwise in *Tamus*, where no more than that part of the hypocotyl which faces downwards takes on growth that makes the tuber. In the limitations of the service that the cotyledon does Dioscoreaceae agree with the whole of the Liliaceae except the Allioideae where the cotyledon frees itself and assimilates—a contrast useful for eliminating ideas that Dioscoreaceae could have been derived from the part of the proto-Liliales whence Allioideae came.

The embryos of several species of the Dioscoreaceae have been figured. Adrian de Jussieu figured that of *D. villosa* and of another species presumedly *Rajania cordata* (*Ann. Sci. Nat.* (2), pl. 171, 1839). Beccari figured what he called *D. bonariensis*, probably meaning *D. sinuata* and what he called *Rajania cordifolia*, indicating *Rajania cordata* (*Nuovo Giorn. bot. Ital.* 2, pl. 4). Süssenguth has figured those of *D. caucasica*, *D. sinuata* and *Rajania sintensis* (*Bot. Zbl.* **38**/2, 20, 1921). That of *Tamus* has been figured several times. All the embryos are closely similar; but that of the round-seeded *Tamus* less flattened. Evidently this character came with the rounding of the seed, i.e. is secondary. It must have been that the ancestry of *Tamus* was wind dispersed, and the measure of flatness in its cotyledon is left from that stage.

There is a notch at the apex of the cotyledon of Dioscoreas which has been claimed, along with the double vascular bundle in its petiole, as support for the theory that the cotyledon of a Monocotyledon is two united. Süssenguth, referring to this, names as another species showing the notch *D. hirsuticaulis* (presumedly the form of *D. glauca* so named by Bartlett); and adds that there is no notch in *D. adenocarpa*, *D. quartiniana*, and *D. pyrenaica*.

The base of the cotyledon embraces the cauline end of the embryo and creates a protective pit for it; but there is sometimes a departure from complete embracing (see Süssenguth, *loc. cit.*, pp. 28 and 29). The double vascular bundle was described by Miss Sargeant (*New Phytol.* **1**, 107, 1902; and *Bot. Gaz.* **57**, p. 325, 1904); twin strands, being as she says, widespread in the Monocotyledons, the possession of them does not point to *Dioscorea* having a peculiar place in the phylogeny of the Monocotyledons.

Throughout the Liliales, Juncaceae excepted, the food stored in the seed is cellulose in a form which differs from what is usual in the way in which it takes stains. It is the cellulose of the date stone (see Gardiner and Hill in *Proc. Camb. Phil. Soc.*, **11**, 445, 1902). Celluloses are slowly digested from seeds, much more slowly than fats and very much more slowly than starch. Coulter has commented (*Morph. Angiosp.* p. 226, 1903) that the Liliaceae combine the storage of cellulose with a wider dispersal in the World than, for instance, the Farinales which store starch, and he suggested that the adoption of cellulose has favoured dispersal by providing a seed more suited to travel. Dioscoreaceae doubtfully support this line for the species tend to be of rather restricted dispersal; but there is a reason for this—the travel of dioecious plants must be not only in pairs but in the right pairs and that means an outweighing handicap.

The agent for its travel is the wind and the wind is an unreliable servant. It is more often either too weak or too strong than at right strength. The dwarfs in *Dioscorea*, after suiting themselves to doing without tree-cover in quite a number of cases, found it profitable to diminish the area of wing which enabled the wind to carry them far. *D. pyrenaica* illustrates this. For establishing themselves its seeds must not be carried beyond the screes and creviced limestone faces of their mountains; they need to be dropped into a cranny. There is another species of *Dioscorea*—*D. longicuspis*—whose travel-adventuring seeds lose the wing by the moistening of an absciss line if the seed alight on a wet surface. *Tamus* is not unlike *D. pyrenaica*, and indeed related to it, in its abandonment of wind dispersal. Its fruits, not drying for dispersal, retain the seeds, keep fleshy for a long time, and the seeds have come to possess a very slow after-ripening, the first part of which is spent within the juicy fruit and the second in working a way into the soil by alternate swelling of the seed-coats and shrinking as they dry (for a full description of this see *J. Bot.* p. 44, 1939). Another species which buries its seeds is *D. (Epipetrum) humilis.* This plant seeks to press its whole nearly globose capsule into the soil, screwing it forward by the pedicel becoming spiral.

Apart from these the family uses commonplace methods, and is as the Liliaceae. A few records suggest that germination is normally prompt; records exist of this for *D. bulbifera*, *D. pentaphylla*, *D. hispida*, *D. laurifolia*, *D. glabra*, *D. wattii*, *D. orbiculata*, *D. pyrifolia* and *D. humilis*.

After germination the seedling is in urgent need, for its inherited small store of food is depleted, and it faces a short season and a period of rest. It needs light and goes through what is perhaps its greatest testing period. To get light preference is given to the first leaf which is provided with a long petiole and a lamina of full shape. The growth of a second leaf is as a rule delayed for the benefit of the first. In the next period of growth a short length of stem is produced and then its further extension arrested. When the arrest appears, the leaf of the node pushes the arrested end aside just as the cotyledon pushes the cauline end of the embryo aside.

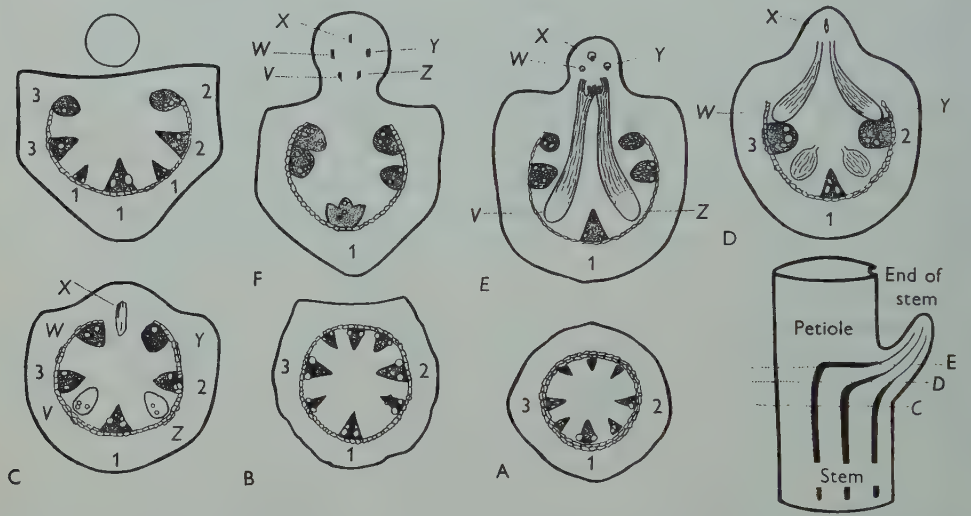

Fig. 49. Sections through the first stem of a seedling of *Tamus communis*. A, at the base, where the weak stem is thinner than above; B, with shoulders in anticipation of the node above; C, the sclerenchymatous sheath open and bundle X from the second internode is seen entering the ring; D and E, the bundles V, W, Y and Z also enter the ring by crossing between the base of the petiole and the top of the lower internode. The diagram on the right of the lower line suggests their courses. F is above the severance. The pectination is perfected; but an examination of other stems has shown that it is not unusual for bundle X to fail.

Fig. 49 shows the result in *Tamus* with the displaced end of the stem providing cauline bundles for the stem. Dispossession by the one leaf is forcible; the cauline bundles have to cross the node; they provide some facts of interest regarding the node itself. In crossing they thicken slightly and their thickening may be regarded as representing an unprovoked ganglion; and the circumstance may be recalled that the bundles in the palms thicken a little at the top of their curve into the heart of the stem. The reader will recall that the vascular bundles are figured as being eight in number in the new stem of *D. opposita* (Fig. 33, p. 363); here again in *Tamus* we find eight. This number is really basic. Ascending the stem components A, B and C keep the number constant, but B as approaching the node shows the outline of the stem slightly disturbed. Component C forward shows the bundles 1, 2 and 3 passing into the leaf: they are the common bundles of the leaf trace of the solitary leaf. Components C, D and E show five cauline bundles taking their places between the common bundles and the lower right-hand diagram indicates their crossings. In component F the foliar bundles and bundles from above are separate; and those of the petiole are branching, the median into three and the laterals into two.

There is nothing in what the seedling exposes which supports the idea that the Dioscoreaceae possess a palm-type vasculation in the stem.

The cauline bundles *V*, *W*, *X*, *Y* and *Z*, seen as exceeding small in component F, gather size as soon as they enter the stem, which shows that the node is a stage-post and their function given them node by node. Reference may now be made to *J. Linn. Soc.* (*Bot.*), **53**, Fig. 46 on p. 364. The figure is of the exhausted apex of a stem of *Tamus*, just leafy; and it shows the production of common bundles not pectinated with cauline bundles. This and what has been recorded of the seedling indicate that pectination holds no mystery but is simply a consequence of the need of the two kinds of bundles and a result of the way in which the bundles appear. The rule that not more than two common bundles shall run parallel is not observed in poor development for three do so in that figure.

§30. *The glands of the stem and leaf*

In 1850 Sigismund Kunth published (*Enum. Pl.* **5**, 352) the name *Dioscorea glandulosa* which Klotzsch had put against a specimen having what he took quite rightly to be glands scattered in the surface of the stem and leaf. In 1882 Thomas Bokorny called attention (*Flora*, **65**, 343, 1882) to the way in which discoloured spots appear on leaves of other species in drying as in a plant-press. The spots proved to spread from glands. Soon after this Delpino and Correns independently investigated these glands, Delpino seeking for causes of visits from ants to plant surfaces and Correns undertaking an anatomical study. Questions as to the names of their species arise.

Both made use of *D. bulbifera* and applied the name rightly; both made use of a species of the section Enantiophyllum, but neither left exact proof what their Enantiophyllum was; Delpino called it *D. sativa*—a name much confused and at times applied to *D. alata* which perhaps is what he had. Correns claimed to have drawn most of his information from *D. batatas*—(its legitimate name is *D. opposita*); but most of his figures were obtained from *D. bulbifera*. In his search for material he drew on the Botanic Gardens of Graz and Munich (*S.B. Akad. Wien.* **97**, 654). Correns had found at Graz *D. bulbifera* and *D. opposita*, the first under the name '*D. sativa*'; then at Munich he found *D. bulbifera* under its proper name, along with *D. opposita* under the name *D. decaisneana*; and he found a third plant called '*D. sagittata*'. It is not possible to put a firm name to this last: De Wildeman who attempted to do so (*Diosc. alim. et tox.* pp. 15 and 20, 1938), makes two incredible guesses.

Delpino suggested that *D. bulbifera* is myrmecophilous, and assumed the glands to secrete nectar (*Mem. Accad. Sci. Istit. Bologna*, **8**, 46; 1888). Correns proved more reliable; for though he suspected the secretion to be nectar, he admitted that he had not proved it to be. His microscopic investigations showed the origin of the surface glands to be in a single epidermal cell which, dividing, pushes its proliferation into the tissues below it without losing the surface for discharge. These glands which he figures excellently, have much more of their surface inwards that is exposed to the air; they are plano-convex (see Fig. 50A). It is not yet clear that they are more than safety valves, whereat ants and other insects can get a drink. They serve during the most active growth of the young leaf and are later cut off by a suberized coating in a way which shows that their function is physiological. The glands of the whole of the section Enantiophyllum are large and go deep (Fig. 50B); and they have a vastly greater surface in contact with the parenchyma about them, and a defined pore for discharge.

Queva was the next botanist to pay close attention to the glands; this he did in his lengthy paper (*Mem. Soc. Sci. Lille.* (4), **20**). He used *D. bulbifera*, as Correns had done, and he called its glands appropriately discoid glands. Though he named eight species as carrying glands, he made no comment on those of large size. Some species, he stated, do not have glands, i.e. he did not find glands. The next writer was Hansgirg who indicated the presence of glands in *D. laxiflora*; and he was followed by Bergmann who (quoted here from *Just's Jahresber.* **1913/2**, 1154) wrote of the glands of *D. dodecaneura* using the synonym *D. discolor*. Orr followed with a more detailed paper (*Notes Roy. Bot. Gard. Edinb.* **15**, 135, 1926), wherein he made it clear that the taxonomist must pay attention to their presence or absence, and to their size and depth. I hope that the following statement of their known occurrence is complete, but must add that to prove their absence is difficult; that is why Winckler (*Ber. Dtsch. Bot. Ges.* **43**, 590, 1925) could report glands in abundance in *D. elephantipes* after other observers had claimed that this species has none. This is my list:[1]

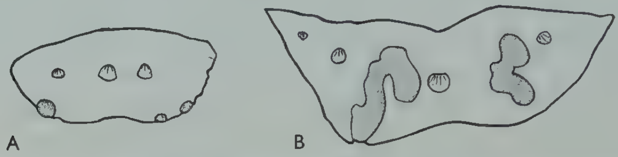

Fig. 50. **A,** The superficial glands in the fore runner tip of *D.* (*Lasiophyton*) *pentaphylla*; B, the deep glands in the fore runner tip of *D.* (*Enantiophyllum*) *pyrifolia*. Along with the glands, the vascular bundles are indicated. From drawings by Major M. Y. Orr.

(i) *Dioscorea*: Old world species by sections alphabetically:
COMBILIUM. *D. esculenta* O, under synonym *D. fasciculata*.
ENANTIOPHYLLUM. *D. alata*, O; *D. cayenensis*, O; *D. glabra*, O; *D. kingii*, O. as *D. porteri*; *D. laurifolia*, O; *D. nummularia*, B; *D. opposita*, C; as *D. batatas* and presumedly also as *D. decaisneana* and Q as *D. batatas*; *D. orbiculata*, O; *D. polyclades*, O; *D. puber* B; *D. pyrifolia*, O; and Q *as D. repanda*.
LASIOPHYTON. *D. hispida*, O; *as D. triphylla*; *D. pentaphylla*, O; *D. scortechinii*.
OPSOPHYTON. *D. bulbifera*, C, D, O and Q.
PARAMECOCARPA. *D. piscatorum*, O.
TESTUDINARIA. *D. elephantipes*, W.
and *Stenomeris dioscoreifolia*, O.
Tamus communis, Q.
(ii) *Discorea*: New World species by sections
BRACHYSTIGMA. *D. sinuata*, Q.
CRYPTANTHA. *D. laxiflora*, H.
DEMATOSTEMON. *D. adenocarpa*, C; *D. campestris*, C.
LASIOGYNE. *D. dodecaneura*, B and O as *D. discolor*; Q as *D. illustrata*.
STENOPHORA. *D. villosa*, C.
STRUTANTHA. *D. amarantoides*, O, and Q as *D. multicolor*.
TRIGONOBASIS. *D. convolvulacea*, O.

Orr examined the leaves of several species of the section Stenophora without finding any; and therefore Correns's statement that *D. villosa* has the glands wants confirmation. The section seems to be without glands.

The surest place in which to find them is the fore-runner tip; secondly, the back of the lamina close to the very base. They may be on the petiole and are sometimes freely present on the stem just below the origin of a leaf. Orr found them on the face of the lamina of

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[1] Authorities are: Bergmann, B.; Correns, C.; Delpino, D.; Hansgirg, H; Orr, O; Queva, Q.; Winckler, W.

D. amarantoides but on the face in no other species. As already said they are differentiated very early. It would seem that they appear when and where required and there is interesting work to be done on the conditions which make them numerous. Delpino, as well as Correns, remarked that their activity is greatest when the leaves are very young. Raciborski suggested a two-stage development for the leaf; first the fore-runner tip, mature and active while allowing the part behind to develop; this is correct only in part; the correct way of putting it is that the glandular function is here developed in advance. Delpino would have it that the glandular excretion keeps the ants from leaving the leaf and that they protect their supply of nectar. If it keeps ants on the spot it keeps other insects also whatever their occupation. On the leaves of *Tamus* in Britain small Psocopterids are common, and it is conceivable that the supply of water does something to retain them, but to no certain purpose. Ants have not been seen to disturb them. Gentner's suggestion (*Flora*, **95**, 328, 1905) that the discharge relieves pressure in still embryonic tissues is the best.

From the evolutionary standpoint the family's need for the glands would not press heavily until there was a stem of some length able to convey water sometimes too rapidly up its rather large channels. The fore-runner tips collectively plug the end of a vegetative bud and keep the interior moist as well as getting rid of those drops of water which travellers in the tropics see in the early morning when the transpiration is brought into opposition with a saturated air. If the bud dries too rapidly the colleters in the bud remain a second defence. Because the apical dominance of the family enhances so greatly the value to the striving climbing plant of the apical bud, that bud's protection has been important enough to have been in the front in its struggle to maintain itself.

It is a fair comment to say that Delpino set to work on the ways of indigenous ants with exotic plants.

Gentner observed stomata to be plentifully associated in the leaf-tip, counting 12–14 in a cluster on a tip only 1 mm. long.

The activity of the fore-runner tip soon wanes, and its growth ceases before the basipetal wave leaves its neighbourhood in its course down the lamina. There is one exception to the cessation of growth, namely the elongation of the tip as we see it in *D. sansibarensis* where a different purpose enters.

In this curious plant, corrugations of the upper surface of the fore-runner tip give rise to chambered slits within which the production of colleters is continued so actively that they remain full of mucilage (see Orr in *Notes Roy. Bot. Gard. Edinb.* **14**, 57, 1923, where the synonym *D. macroura* is used). The cavities harbour nitrogen-fixing bacteria in the mucilage with which the colleters fill them; and, as Orr showed, the nitrogen is passed to the *Dioscorea*.

Recently Miège has shown that the scale leaves low down on the stem of *D. mangenotiana* are not the simple ovate-lanceolate reduced leaves which one expects, but up to 4 cm. long with a trace of a lamina and a very distinct fore-runner tip with its margins incurved so that they make a funnel in which mucilage is accumulated and bacteria live. The duration of these bodies is short (*Bull. Afr. Noir*, **20**, 40, 1958); they perish as the assimilating leaves appear; but the bacteria probably occur up and down the plants where mucilage enables them to live for a while. The bacterium is possibly that species which lives on various species of Rubiaceae.

§31. '*Acarodomatia*'

At the base of the lamina in a few African species of the section Enantiophyllum the leaf-margin is revolute on either side of the insertion of the petiole: and De Wildeman called the galleries made in this way acarodomatia (*C.R. Acad. Sci., Paris*, **139**, 551, 1904). In *D. minutiflora* and *D. burkilliana* the revolute margin bears a curious horn and in *D. smilacifolia* a small shield which deepens the shelter. That acari tenant them, has not been proved and strictly, therefore, *acarodomatium* is a questionable name. In the year before De Wildeman announced his discovery Penzig and Chiabrera had reviewed in detail the subject of acarodomatia (*Malpighia*, **17**, 1903) and they would have withheld it, for they announced that no Monocotyledon was known to have such structures. It was by a little extravagance that De Wildeman contradicted them; but, whether he was right in his guess or wrong, the structure is interesting and unique. Even if acari be found to occupy it, the causes which have led up to the appearance of a revolution original in the Monocotyledons would appear strange: is it possible that strains at the very termination of the growth of the dioscoreaceous lamina should pull the margin into the position which makes a gallery; but what calls out the processes on it? Minute insects that, seeking humid cover, crouch into the angles between the larger primary nerves on the lower face of the lamina would find similar humid conditions in the galleries. De Wildeman may have been right.

§32. *Roots*

As is usual in the Monocotyledons the primary root is short-lived. This we know with reasonable certainty to be the case throughout the Dioscoreaceae in the Old World. It remains to be proved to be true of those in the New. In the Old World species this root is likely to perish unbranched save for roots of similar size which emerge at its very base, from the hypocotyl rather than from it. Later we find the plant possessed of roots of two kinds differing in size—long exploring roots, diageotropic and spreading in the surface soil, and rootlets mainly of short life, to be met with among and below the others. In the section Paramecocarpa the short roots may lignify internally and, the cortex sloughing off, they become thorns which, scattered over the tuber, are protective. In *D. esculenta*, the only species of the section Combilium, and in a few African species of the section Enantiophyllum, the lateral roots of some of the long exploring roots are converted into thorns in the same way. They are not, as the thorns in the section Paramecocarpa, directly on the tubers, but are much more effective by being a few centimetres away. They persist dead in the soil for years and in *D. esculenta* the accumulation makes in time a formidable *cheval-de-frise* defending the tubers. In the species of Enantiophyllum they arch around the sides of the tubers: and because they do this a second factor is seen to have entered into their evolution, namely a positive geotropism in place of the natural diageotropism. All the thorns in these Enantiophylla are of similar length; but in *D. esculenta*, those which point upward and presumedly are those first encountered by a pig in search of the tuber, are longer than the others. I ask the reader if he can explain how such a rare development as thorny roots came into the Palmae as well as into three sections of the genus *Dioscorea*.

Man, with a stick in his hand, finds it easy to turn the defence of *D. esculenta*; and it would seem that he has almost destroyed the wild supplies in south-eastern Asia. It is interesting to discover a case of Natural Selection working against the wild pigs to the profit of wild primitive man.

E. V. Watson found a little starch in the cortex of the roots of *Trichopus zeylanicus* (*Notes Roy. Bot. Gard. Edinb.* **19**, 127, 1936); but the cortex is not a normal place for storage of starch.

Reiche's claim that the tap-root of *D.* (*Epipetrum*) *humilis* turns into a perennial tuber has been mentioned on p. 328.

§33. *The hairs and their taxonomic value*

This heading does not cover colleters: they belong to a passing phase and are gone before hairs become functional.

More than half of the species of Dioscoreaceae are glabrous, and many that have hairs are but scantily clad. None of the para-Dioscoreeae have hairs; nor has the genus

Tamus. But in the genus *Rajania* a few species carry hairs. The hairs of *Dioscorea* in the Old World take a variety of forms; but in the New World there is scarcely any variety except in length. *D. bulbotricha*, a native of Brazil, excepted, they are 1-celled, short or cottony. Handel-Mazzetti figured the hairs of his species with his description in 1908.

I devote here Figs. 51 and 52 to hairs from the Old World, the simpler in one figure, the less simple in the other. Glandular hairs are not carried. The hairs of the African *D. preussii* (see Fig. 52 E) are of a curious shape, so bent and hooked as to appear very effective in the hindering of an insect or the creation of a blanket.

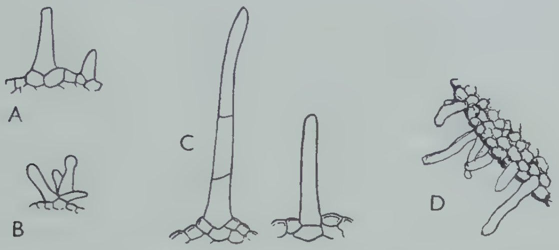

Fig. 51. Hairs in the Dioscoreaceae that are simple. A, The finger-like hair of *D. bulbifera*, var. *anthropophagorum*; B, a tuft of such hairs from *D. antaly*; C, the hairs of *D. glauca*; D, hairs carpeting the underground parts of *D. dodecaneura* functioning as root hairs. All × 20.

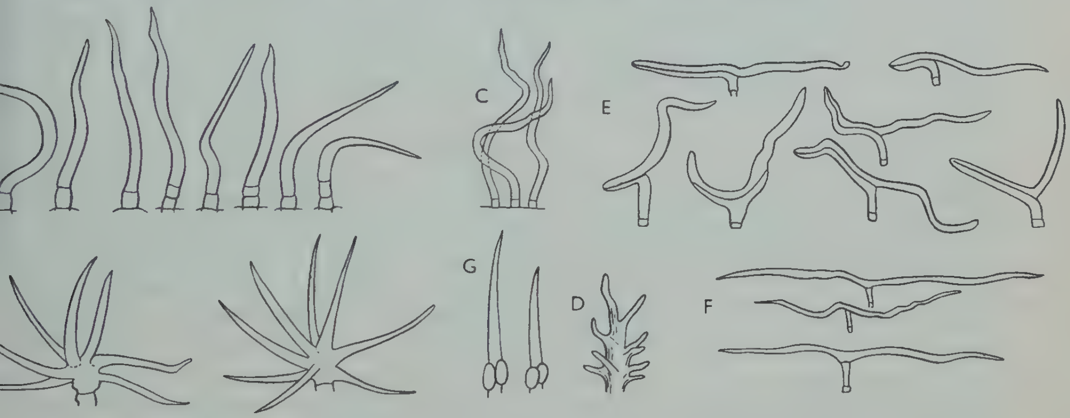

Fig. 52. The less simple hairs of the Dioscoreaceae. A, Hairs of *D. dregeana* and throughout the section Lasiophyton; B, the stellate hairs of *D. longicuspis* and throughout the section Asterotricha; C, the cottony hairs of *D. ovinala*; D, a dendroid hair of *D. orbiculata*; E, the curious hairs of *D. preussii*; F, the T-shaped hairs of *D. esculenta*; G, stiletto hairs from *D. pyrifolia* and the more common form of hair in the section Enantiophyllum. All drawn to the same scale.

The T-shaped hairs of *D. esculenta* (Fig. 52 F) suggest a relationship of *D. preussii* to *D. esculenta* which other characters do not support; the resemblance is probably a case of parallel evolution. On the contrary, other characters than the hairs indicate a relationship between the sections Enantiophyllum and Asterotricha and permit us to regard the stellate hairs of the latter (Fig. 52 B) as of common origin with the stiletto hairs of the former (Fig. 52 B, G). The 2-celled hairs of Lasiophyton (Fig. 52 A) are sometimes so densely set on young surfaces as to make impenetrable thickets; in other positions they often curve and lie horizontal over the epidermis.

The simplest hair that can be found in the Dioscoreaceae is the finger-like outgrowth of an epidermal cell (Fig. 51 A) that occurs on the surface of *D. bulbifera* in Africa, but is entirely absent from the species in Asia. This type of hair occurs in *D. antaly* grouped

(Fig. 51 B) and looking like ragged scales on the back of the leaf along the primary nerves. It may be of interest that the position of such a tuft is over a vascular bundle, appearing as a prickle appears. The finger-like hairs may become 2- or 3-celled without alteration of shape, or may be made taller by subsidiary cells at the base.

To be lifted in this way is different from possessing a lifting cell as part of the hair itself (as in Fig. 52 A). The hair of the section Lasiophyton is very characteristic; its foundation is a cell of the epidermis; then there is an almost isodiametric cell which carries a long and as a rule very acute cell; it does the blanketing. Apparently there is no species in Lasiophyton that does not possess these hairs. Their cell-wall is commonly minutely sculptured, the sculpturing straight in the isodiametric cell and spiral in the long cell. Stiletto hairs characterize the sections Paramecocarpa and Enantiophyllum. Dendroid hairs occur in a few species of Enantiophyllum.

It cannot be without some phylogenetic importance that the complex hairs are found in Asia and Africa, and are absent from America and Madagascar (*D. esculenta* is introduced) which is as if their appearance in the family was not very remote, the first Dioscoreaceae being glabrous, then the next with simple hairs and only after that the complex hairs.

Süssenguth has written (in *Bot. Zbl.* **38**/2, 71) that the hairiness of the Dioscoreaceae brings the Dicotyledons to mind, and is 'probably' indicative of the family having been basic in the evolution of the Monocotyledons out of the Dicotyledons. As the reader already knows I do not agree, as I do not regard the family as in any way basic. It is not that the hairs are ancestral; but that they have appeared in Dioscoreaceae and Dicotyledons from similar living conditions. It has been suggested that the characteristic stiletto shape has been spreading in Malaysia by introgressive hybridisation (*Flora Malesiana* (1), **4**/3, 332, 1951); coming from the direction of India it is now at Weber's line.

§34. *Bulbils*

Bulbils are doubly a feature of the Dioscoreaceae, on account of their size as well as being general. To produce bulbils is a property of many related and unrelated families; a single genus in the Ranunculaceae produces them; an isolated species of the Cruciferae and a single species of the Saxifragaceae. Other illustrations of independent adoption can easily be found; but bulbils are met with throughout the species of Dioscoreaceae with but a small number of exceptions. Of allied families, bulbil production in *Allium* and *Lilium* is general—not of large bulbils, but of bulbils which, the size of seeds, are reproductions of the onion's or lily's coated bulbs. So in Dioscoreaceae the bulbils are miniature reproductions of the rhizome. There is an unmistakable morphological repetition in these Liliales between bulbils on stems and the storage organ underground. A connexion between sex and bulbil production is not proved.

Bulbils are so freely formed in the Dioscoreaceae that their propagation value is indisputable; but they are not known in the para-Dioscoreeae and are all but absent from the section Stenophora of *Dioscorea*. It is unfortunate that they invariably fall from herbarium specimens in the course of drying; and in consequence of the collectors' inadvertences the records of their production are defective.

A bulbil is a branch. As its purpose is dispersal, it should be aerial and distal on the stem. In some species it is dropped partly desiccated and is carried away by water. This is how *D. sansibarensis* behaves. Just before the bulbil's maturity, the bulbil begins to dry and after a little drying becomes buoyant; and it is cut off, falling to the ground in a state ready to be swept to another situation by flood waters, or it falls perhaps into a stream which may carry it far from its place of origin. Observing its floatability I experimented. Bulbils were kept in water for 6 weeks, during which time they did not sink. Satisfied that they float, I took them from the water, planted them, gave them a slightly higher temperature and was gratified to find that all were alive and uninjured. In another experiment I took two slightly immature bulbils which sank in water; they were dried until buoyant, and then placed in a hot-house where they promptly germinated. This manner of dispersal leads to the great abundance of *D. sansibarensis* in certain African valleys.

D. bulbifera likewise has bulbils which float: Guppy made some observations on them (see his *Obs. Nat. Pacific*, **2**, 532, 1906). He tried them in sea water.

Other observations have been made (see *Flora Malesiana* (1) **4**/**3**, 312, 1951); but there is a need for more. Squirrels certainly carry the bulbils for short distances, probably taking them to quiet corners to try if they are edible.

D. bulbifera in particular gains by means of its bulbils a quick way of securing establishment. I have seen a bulbil produced at 6 months by a seedling deprived of water, and it is clear that the arrival in a new situation of a bulbil, say of a male plant, may result in tenancy awaiting the arrival of the female for a period theoretically only terminable by an accident. The bulbil that a 6-month-old seedling can produce is of course very small and the risks large.

Man in the Pacific has long possessed and kept in cultivation a variety with very large bulbils—*D. bulbifera* var. *sativa*—which was brought into India from farther east in the middle of the last century and to Europe later. There is a full account of it in the *Ann. R. Bot. Gard. Calcutta* (**14**, 119, 1936). Either this or the somewhat similar var. *suavior* was the subject of Dale's paper in the *Ann. Bot.*, (**15**, 491, 1901) and of Goebel's investigations. Dale claimed the bulbil and the tuber to be morphologically identical; Goebel (in *Flora*, **95**, 179, 1906) called the bulbil an arrested condition—Hemmungsbildung—of the tuber. This it is not; we have dealt with the tuber as a swelling either of the hypocotyl or of a part of it; and the bulbil is not an arrested condition of this but is a whole branch with its elongation under a modified arrest and with leaf-production forbidden, with the orderly disposal of leaf-serving vascular bundles confused and vasculated as in the tuber by irregular strands. Hypertrophy of the storing tissue apparently leads to this irregularity. The bulbils do not have the cortical growth which underground parts have, but last as long as the lobes of the underground tubers. With a like purpose, they must have had an unlike evolutionary history. It is a legitimate hypothesis that the orderliness of the bundles within an internode of the stem is a direct consequence of the orderliness of emergence-production at the apex; then the apex of a bulbil, which is due for study, presumedly should be disordered.

Bulbils and tubers come into competition for food to store; and *D. bulbifera* var. *sativa*, which has been mentioned above, has reached the limit of storing all its food in bulbils so that it has no storing tuber. The species is predominantly bulbiliferous and has varieties in each possible state from abundance of bulbils to few. The most bulbiliferous are cultigens as is disclosed when it is realized that the bulbils are less nauseous than bulbils usually are and even pleasant to eat after cooking; but Man did not select it for abundance of bulbils: he found it and adopted it for cultivation; and then would begin the selection. Asia holds other varieties variously useful and productive of bulbils. Africa holds more; and it is interesting that their bulbils differ from the Asiatic in shape, growing angular as they grow larger. All these African races at the present time must remain under var. *anthropophagorum* until they have had careful study in cultivation. Some of them seem to be much more poisonous than others; it is evident that selection has been done in Africa as well as in Asia. It is also evident that the original material that Man had for his use differed; and different material led to morphological differences. The ridges which make the angles, consist of ranked vegetative buds touching one another. If one bud be blinded experimentally when the bulbil germinates, the next at once takes its place. The lines of buds are on the parastichies.

There is no reason to think that Man has selected any other species for bulbils. Some clones of *D. alata* produce them at times in great quantities. Rheede wrote of fattening swine on them, but no one has supported him. Doubtless the wild pigs eat them.

In as much as bulbils are promoted when the fluids of the stem are interrupted, large production may be accidental. When an experimenter in France tried to multiply his stock by laying the stems of *D. opposita* on the soil and fixing them there, he provoked a supply of bulbils instead of roots, apparently as a consequence of obstructions by the bending of the stems. Towards the time of a stem's natural death other and natural obstructions may arise which give to formed bulbils an increased amount of assimilates.

Bulbils possess the polarity natural to a stem. Goebel examined it in *D. japonica* (*Flora*, **95**, 179) and I have done so in *D. bulbifera* (*J. As. Soc. Bengal* (N.S.), **7**, 467, 1911). It favours the lowest buds.

The Dioscoreas which produce bulbils freely do not spread into trying climates as far as the family goes. Northwards from China *D. japonica* ceases where Manchuria is reached, but *D. nipponica* which is without bulbils passes beyond to the Amur. In the Himalaya *D. melanophyma*, producing abundant bulbils, ceases 2100 metres below *D. deltoidea* which does not produce them. In South Africa the Testudinarias which resist drought so well do not carry bulbils.

It is very general in the Dioscoreas for three buds to appear in a column within the protection of an axil: if there is to be a bulbil as a rule only one bud is committed; but we find two sometimes in *Dioscorea alata*; and sometimes the two may coalesce at the base. Rarely, and probably only under extremely moist conditions, bulbils are found with roots extruded. The conditions for this have not as yet been experimentally examined.

The cork which seals a bulbil renders it fawn-coloured; but in some species the bulbil becomes purple-black. In the latter chlorophyll seems absent; but when the bulbil is fawn-coloured chlorophyll is not excluded.

Bulbils are of little use as food; they are generally more poisonous or more nauseous than the parts of tubers which man eats. As bulbils are transformed branches of annual stems it needs to be asked if the enforced rest makes them live longer. This seems not to have been tested.

The taxonomist welcomes information of their occurrence; he should equally welcome information as to their size; for a family it is their size more than their presence which is a family feature.

§35. *The inflorescence*

It is convenient to turn from the bulbil which is a whole branch committed to one purpose, to the inflorescence which is the like. A salient fact is that the commitment is sharply limited at the very origin of either, and that this is largely attributable to a distal influence: for the bud in either case has been under apical dominance and when released is reliant on an already ageing parental stem. It is no wonder that the delimitation should be definite. This age-delimitation accounts for a lateral branch being thinner than its parent at the horizon of taking off and for the leaves of the lateral branch being smaller than those of the axillant leaf and yet again for the lateral branch having a smaller apex with consequent alteration of divergence of its earlier leaves. The reader will find data for *Tamus* in an earlier paper (*J. Linn. Soc.* (*Bot.*), **53**, 373). The distal end of an inflorescence is likely to be as abrupt, to die with its last flower lateral to its tip.

Observations made on *Tamus* in the south of Britain suggest that the ratio of male to female flowers in the countryside is about 60 to 1. Putting out this excess of males is the price which the species pays to secure its reproduction. In the first line there are more male plants than female, in the second more inflorescences carried on a male plant than on a female plant, in the third there are more flowers on a male inflorescence than on a female. the whole working up to the ratio given. The greatest contribution is in the proportion of flowers on the inflorescence. Most of the species of *Dioscorea* raise the proportion by carrying cymes in the place of single flowers along a raceme or spike. Fig. 53 illustrates these cymes. The cymes are invariably few-flowered and fewer- and fewer-flowered from base to apex. The cymes rarely disperse the flowers composing them, but by being closely constructed intensify whatever attraction the flowers offer where they are. The species with cymes expose twice or thrice or more times as many flowers over a given length of inflorescence than the racemes or spikes.

In the writer's opinion, the panicle that is seen in some species of the section Stenophora, and in the genus *Tamus* is primitive for Dioscoreeae; neat racemes of solitary flowers, neat cymes in series and spikes uniform from base to apex bear the marks of selection from this. Whether this be right or not, the characters are taxonomically useful.

Dwarfing makes massing impossible, and the small number of flowers make no defined inflorescence. The female inflorescence exhibits no characters that are taxonomically useful. But the curious circumstance that *D. paradoxa* carries only a single capsule in each inflorescence must not be passed unnoticed. Is the fertilized flower rendered dominant over the buds of the unopened flowers in its neighbourhood? The fertilized flowers of *Trichopus* seem to possess this power. The way in which field collectors bring the male and overlook the female, and the most cursory examination of the two sexes in herbaria abundantly demonstrates that it is a family character for the male to be in excess.

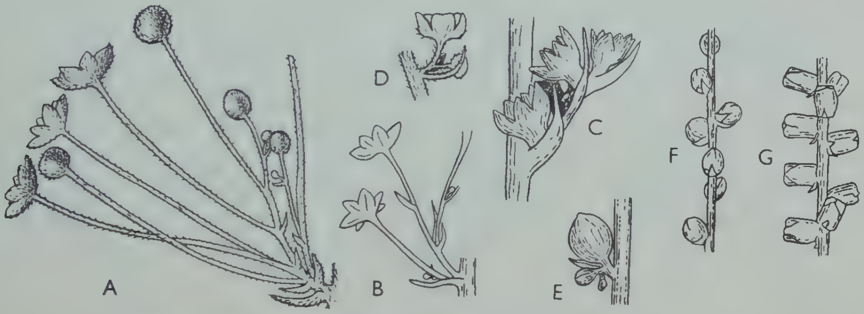

Fig. 53. A–E, cymes of male flowers such as are produced laterally in panicles; F and G, spikate male flowers; all × 5. A, of *D.* (*Brachyandra*) *sambiranensis*; B, of *D.* (*Madagascarienses*) *arcuatinervis*; C, of *D.* (*Shannicorea*) *pseudo-nitens*; D, of *D.* (*Cardiocapsa*) *mamillata*; E, of *D.* (*Illigerastrum*) *simulans*; F, of *D.* (*Enantiophyllum*) *liebrechtsiana*; and G, of *D.* (*Enantiophyllum*) *odoratissima*.

Stem structures that support the flowers are of two kinds—pedicels and pediments. The reader is referred to the paper on *Tamus* (*J. Linn. Soc.* (*Bot.*), **53**, 327, 1949) where swellings of the stem under foliar emergences are described; these swellings are pediments; and again to the swellings at nodes in *Paris* (in this paper, p. 346) and at nodes in *Dioscorea* (p. 362). Slight exaggerations of these are found in various other Dioscoreas but in the section Lasiophyton conspicuous elongations occur which carry bract and flower to as much as a centimetre from the point of origin (see Fig. 54, components J, K, L and M for illustrations).

The section Lasiophyton is unique in the size of its pediment in certain species.

§36. *The flowers and insect-pollination*

Fig. 54 is devoted to the shape of the male flower and the text which follows to its adaptations towards insuring that insects shall pick up pollen. All the components of the figure are at the same scale and collectively bear witness to the uniformity of smallness in the flowers of the Dioscoreeae. The para-Dioscoreeae are in contrast, for their hermaphrodite flowers are conspicuously larger. There is nothing unusual in reduction of size of flower when one sex is missing; the female flowers of gynodioecious Labiatae, for instance, are smaller than the hermaphrodite. Damaging to the chances of pollination as the loss of size would seem to be, it nevertheless happens; but then do insects which favour the Dioscoreaceae visit by sight? An interlocking of greater size with bisexuality clearly characterizes the flowering plants.

There is in tropical America a section of *Dioscorea*—Macropoda—that exhibits a tendency towards relatively large flowers and a tendency to be abnormal in the sexual organs. It is to be kept in mind.

The largest flower of the Old World among the Dioscoreeae is that of *D. buchanani*—7 mm. across the mouth. The reader should note this dimension, for the herbarium worker, flattening it, forces it to be 9 mm. across. The smallest flowers of the Old World are those of the Madagascan *D. nako*—only 1 mm. across. There are flowers equally small in some American species.

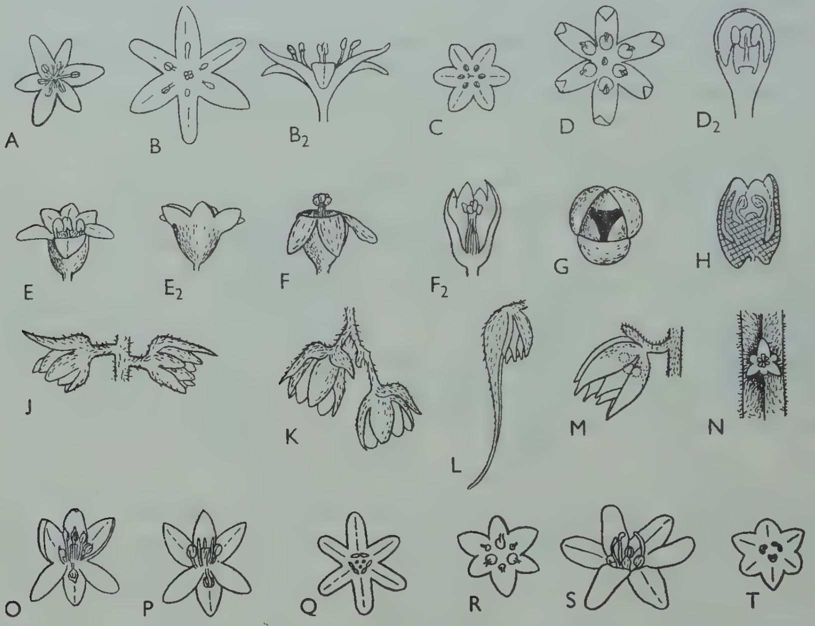

Fig. 54. Male flowers of *Dioscorea*, all × 5, the upper two rows with six fertile stamens of similar size. A, *D. bulbifera* in which the disk is not developed; B, *D. elephantipes*; C, *D. sambiranensis*, and D, *D. mundtii* in which the disk lies open to the sky; E, *D. paradoxa* and F, *D. acuminata* in which the torus is converted into a bell; G, *D. luzonensis*, in which the whole flower is a small water store and the interior kept humid by the enclosing perianth; H, *D. sexrimata* in which the fleshiness is extended upwards. J to N of the third row, flowers of the section Lasiophyton showing the pediment: J, *D. kamoonensis* var. *engleriana*, and K, var. *straminea*, both showing the bract and bracteole lifted up by the pediment to a position in which they seem protective against drip; L, *D. crinita* with a long and ornamental bract; M, *D. retusa* with a small bract seemingly useless when anthesis has been reached; N, the flower of *D. ovinala* set deep in hairs on a winged axis. Fourth row: flowers in which the upper stamens are small or staminodal; O, *D. hirtiflora* var. *polyantha* showing filaments of two lengths and anthers of two sizes; P, var. *trapnellii* in which the ante-petalline anthers are absent; Q, *D. simulans* and R, *D. daunaea* with anthers of two sizes; S, *D. preussii* with long staminodes, and T, *D. arcuatinervis* with three anthers.

The merism is remarkably constant—$K_3C_3A_{3+3}\overline{G}_3$ or $K_3C_3A_{3+0}\overline{G}_3$. I assume Hauman's *D. monandra* to be an abnormality (see p. 320). The sepals which function as cover are just so much larger than the petals as to serve the purpose. The stamens possess not a little variation in the way of presenting their pollen and in the length of their filaments: sometimes these are forked; the upper three if they be sterilized usually serve in limiting the movements of visiting insects, i.e. they are determinants in pollination. If there is sterilization it is invariably of the upper three. Though their sterility borders on the sterilization of the female organs, it is scarcely sound to invoke invading sterility until we can also explain the female flower's loss of staminal fertility. Approximate fixity in the merism is associated with a wide range of form in the torus—both inherited characters which appear in the Liliaceae also. The torus is always with tips that would carry stigmas in the female flower; they are present even in the American section Monadelpha between the anthers, and this shows that the section's fleshy column carrying the anthers is torus. By fleshiness it helps to keep the flower fresh when open.

An enlarged torus is seen in B, *D. elephantipes*, in C, *D. sambiranensis* and in D, *D. mundti*. A concave torus is seen in E, *D. paradoxa* and F, *D. acuminata*. The last two components in the second row show the torus as a small water-store, the species being G, *D. luzonensis* and H, *D. sexrimata*.

In the third row J, K, L and M represent different species of the section Lasiophyton in which a pediment is substituted for a pedicel. The torus is small and the fertile stamens three. They are overshadowed by staminodes and close against the base (note their outline dotted in M). The bract shelters the flower through anthesis in J, K and L; but in M only when very immature.

The lowest row in the figure is of flowers which, like the species of Lasiophyton, have partial sterilization. The way in which the staminodes serve as baffles will be seen.

There are species with the fertile stamens three only in all parts of the tropics but the sections for which the reduction is recorded in the New World are more than in the Old. The number is 18; a little revision might bring it down to 15, for too many sections have been made; but still the number will be above that for the Old World. This reduction of fertile stamens is not a firm sectional character: it occurs in a single species of Enantiophyllum, otherwise normal; in one species of Rhacodophyllum; in a few species of the section Stenophora closely allied to species with six fertile stamens; it occurs in half of the species of Lasiophyton.

Uline and Knuth gave too great importance to staminal sterility, and some of their sections are reducible, for instance Strutantha to Cryptantha, and Periandrium to Sarcocapsa.

Insect-visitors to the flowers of *Tamus communis* have been recorded for England (*Proc. Linn. Soc. Lond.* **157**, 99, 1946); and Brenner has taken note of some seen visiting in Switzerland. Beyond all doubt the insect-visitors in the case of this plant are numerous enough and effective. No insect-visitors have been recorded for other species because no one has sought for them. But that the whole family is entomophilous is quite evident from the structure of the flowers. As the drawings in Fig. 54 are all at the same magnification and, as the reader will gather, are not very dissimilar in size, pollinating agents should be of dimensions that we can deduce from the figure. They are likely to be similar to Thrips or perhaps on average a little larger.

Fig. 55 is of a greater magnification than to those in Fig. 54 on account of its complexity. It is the flower of *D. hirtiflora*; the ellipsoid bud spreads its sepals slightly at flowering; but the petals are held at the tip by entangled hairs, below which they are able to open in a long narrow crack by which insects may enter. The insects having entered find their way to the base of the flower between rather large staminodes and large similar sterile stigmas. The width of the entrance slits—there are of course three—and the spaces between the encumbrances within the flower tell us what the size of the insects must be. The three fertile anthers lie like eggs in a nest at the base on short incurved filaments often, but not consistently, curiously humped at the back with a hump in a similar position to the process on the stamens of *Stemona*.

In the New World occur Dioscoreas with the torus spread flat about the centre of the flower as a rather thick food furnishing area for visiting insects. Whether it excretes nectar and is worth licking or invites penetration is unknown. It is apparent from the study of *Tamus*, referred to above, that tissue-puncturing visitors play a large part in pollinating *Tamus*. The tissue which they puncture is watery.

The insects which pollinate the flowers of the Dioscoreaceae, wherever in the Old World they be, must be flying insects because they have to take to the air to get from a male to a female plant. The reader's attention is now directed to Fig. 54 N which shows a flower of *D. ovinala* set among hairs such as make an approach by air much more easy than an approach by crawling.

Actinomorphy being invariable in the Dioscoreaceae, an insect in approach meets the organs of the flower equally from every side; and there are but few species in which the six anthers do not stand at the same level. A loss of fertility in three of the stamens usually means a slightly widened gap between any two positions of pollen-presentation; but curiously in the sino-burmese *D. collettii* the three fertile stamens have forked filaments and a half-anther is placed in each of the six normal positions of presentation. There are forked filaments which apparently do the same service in the American section Heterostemon.

In passing, one may ask oneself if there is any phylogenetic connexion between the prevalence of extended connectives in the para-Dioscoreeae and the appearance of enlarged staminodes in such African Dioscoreas as *D. hirtiflora* and *D. preussii*. As to *D. hirtiflora* the application of the stamen suggests elongation, but a study in life is desirable.

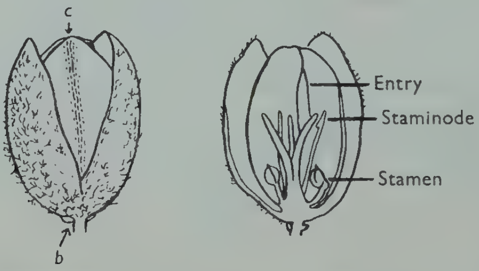

Fig. 55. The flower of *D. hirtiflora* showing its pollination method; × 12. *b*, base of bract above a short pediment; *c*, position of hairs which catch together the three petals and are at the end of a slightly strengthened line down the middle of the petal.

The female flower of a *Dioscorea* is best described, and not untruly, as an alighting platform presenting the stigmas; it too invites study. In a few species the flower expands on the top of a pseudo-pedicel, so completely sunk into the real pedicel are the ovules.

§37. *Fruiting*

The proto-Dioscoreaceae, bridging the Ages from the proto-Liliales to the Dioscoreaceae, passed forward two characters, namely a tri-locular ovary and the presence of two ovules in each loculus. While they were doing this they shaped for the future two other characters, namely recourse to the wind for dispersing the seeds and a dehiscence as the way of launching the seeds for their adventure. They followed this by shaping the seed so that it should have a larger surface to catch the wind. Our immediate interest now is to inquire how tenaciously these four qualities have been retained.

The retention of the tri-locular ovary has been absolute. There is no sign of a side-stepping as, for instance, into the tetramerism seen in Liliaceae (*Paris*) and in Stemonaceae.

The retention of the character of limiting ovule-production at two has not bound *Stenomeris*; and Uline's discovery of three and four ovules in the loculi of a *Dioscorea* on which he founded his genus *Higinbothamia*, exposes a short step in the same direction. No others are known.

It is 60 years since Uline discovered the four ovules of his *Higinbothamia synandra*; but, so slowly has knowledge of it grown, we do not know as yet more about it than that the male plant is identical with *D. gaumeri*, and it seems safe to assume that the female which Uline had should be referred to that species.

The name *D. synandra* has been used for it and would serve for it were it not that the adjective is pre-occupied. Retention of reliance on the wind, while general, has been abandoned in *Tamus* and *Trichopus* (these produce berries) and in *D. humilis*, i.e. the species on which the genus *Epipetrum* was founded by Philippi.

Every genus which has, so to speak, strayed away from *Dioscorea*, is very poor in species. We cannot maintain that they are small from newness; but must hold them small because conditions became hostile, crushed out of existence their links with the more successful part of the family and left them confined within narrow limits.

The character of a dehiscent capsule presenting winged seeds for carriage by the wind has undoubtedly been of great profit to the family and therefore is to be explored for indications of phylogeny. Fig. 56 has been arranged to help in this.

Wings sometimes surround the nucleus of the seeds entirely; seeds with such are in the upper part of the figure. When they are evenly spread the seeds can glide on a very light air. The same gliding is possible if equal wings are at opposite ends of the seeds. Quite diverse in action are seeds with wings extended from a limited part of the circumference: they set the seed whirling in a gusty wind and are ineffective in still air. The seeds so winged are not the seeds of the big forest Dioscoreas; but of Dioscoreas of lower forest, thin forest and scrub. In the high forest it is of small moment when the seed leaves the capsule on its gliding journey, but in the open forest the moment of a gust is best and therefore the presentation of loose seeds in an opened capsule. The last component of Fig. 56—being the capsule of the highly successful *D. hispida*—shows how the dehiscence begins. With the drying which causes it the seeds fall from the placenta, and lying free await the jerk which throws them out. In some Dioscoreas, such as this, the nucleus of the seed is raised to the rim of the cup by the firmness of the wing; in other species the wing is produced upwards and the seed is dragged out after it. There is no doubt as to which is likely to be the more effective; it is the form with the nucleus above the wing. In keeping with the variation in position of the wing there is variation in the position of the ovule on the placenta—should it be near the base or near the middle (seeds winged all round) or towards the apex?

Knuth has written that wings all round would precede wings from a limited part of the nucleus and that is assuredly right. Evolution, to fit the nucleus for carriage, lightened it, and that the wind might carry it reasonably far flattened it. It was inevitable that the sharp edge of the flattened nucleus should provide the wing, and that the first wings would be from the edge at large. Further evolutionary adaptation led away from this in two lines, one that the seeds might glide and the other that they might make the best use of gusty winds. The first led towards the neat wing of Enantiophyllum in a central position within the capsule, and the second to the neat wing of Lasiophyton, and the seed's balance at the mouth of an upturned capsule held up by its wing. Such sections as Stenophora and Testudinaria carried on with increased size of wing, but neglect of moving the position on the placenta forward. The reader will observe that three lines have to be recognized. Sigismund Kunth in 1848 did not see clearly that the last and the second differ, but the seed gave him the best character that he had, and he cut out of *Dioscorea* his genus *Helmia* being the second and the last. Later workers in Berlin such as Uline and Knuth endeavoured to make '*Helmia*' more consistent and to use it as a subgenus. I would abandon it. Of the components of Kunth's *Helmia* it must be said it is not possible that seeds winged towards the base of the loculus were an evolution from seeds winged towards the apex of the loculus; but both would come out of a state of uncertainty such as the section Stenophora has—a state that is illustrated in the plates of the *Ann. Roy. Bot. Gard. Calcutta*, **14**. It is reasonable to see in the wings of species of the section Shannicorea a tidying of such wings. The seeds of the genus *Stenomeris* and the section Paramecocarpa of *Dioscorea* are also tidyings of the same. The seeds of the sections Opsophyton and Lasiophyton are transferrings upwards of placental position as well as tidyings.

It is a disappointment that want of material prevents a comparison here of Old and New World sections.

It will help the reader if the components of Fig. 56 be looked at in turn. A and B are balanced gliding seeds of tropical Africa; then follow other gliding seeds of the tropical Old World. N, O and P are seeds winged upwards. With Q begin the seeds winged downwards. In Madagascar one of the two groups that occur there has a vestige of wing round the nucleus, but the greater part of the wing is downwards; these are seen

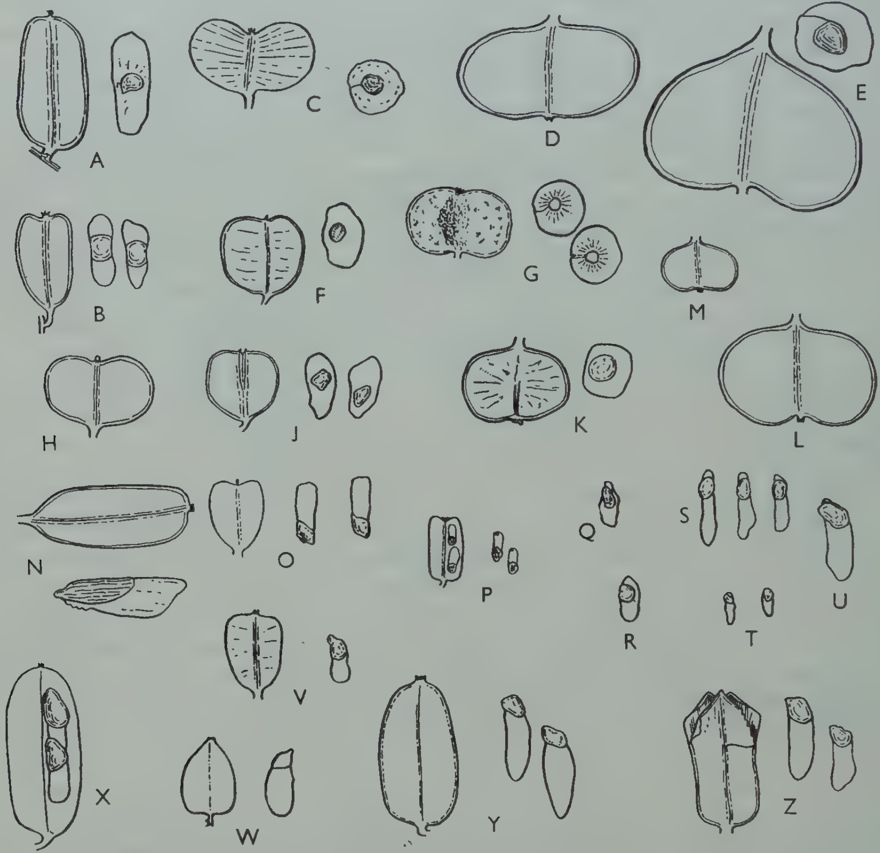

Fig. 56. Capsules and seeds of various species of *Dioscorea*, those with gliding seeds in the upper half of the figure; those with whirling seeds in the lower; the sections indicated and the capsule's position indicating whether reflexed or not. × ½. A, *D.* (*Macroura*) *sansibarensis*; B, *D.* (*Rhacodophyllum*) *rupicola*; C, *D.* (*Madagascarienses*) *arcuatinervis*; D, *D.* (*Enantiophyllum*) *spicata*; E, *D.* (*Stenocorea*) *sumatrana*; F, *D.* (*Stenophora*) *caucasica*; G, *D.* (*Asterotricha*) *semperflorens*; H, *D.* (*Asterotricha*) *hirtiflora*; J, *D.* (*Asterotricha*) *schimperiana*; K, *D.* (*Enantiophyllum*) *abyssinica*; L, *D.* (*Enantiophyllum*) *wattii*; M, *D.* (*Enantiophyllum*) *brevipetiolata*. With this ends the series of species with gliding seeds. *D. brevipetiolata* is inserted to indicate the range in size of capsules in the section Enantiophyllum from *D. spicara* to it. N, *D.* (*Paramecocarpa*) *flabellifolia*, with seeds winged as are those of the genus *Stenomeris*. O, *D.* (*Testudinaria*) *sylvatica*; P, *D.* (*Shannicorea*) *pseudonitens*; Q, *D.* (*Brachyandra*) *analalavensis*; R, *D.* (*Brachyandra*) *pteropoda*; S, *D.* (*Brachyandra*) *sambiranensis*; T, *D.* (*Brachyandra*) *hexagona*. U, *D.* (*Brachyandra*) *seriflora*; V, *D.* (*Brachyandra*) *bemandry*; W, *D.* (*Lasiophyton*) *knuthiana*; X, *D.* (*Seriflorae*) *tsaratananensis*; Y, *D.* (*Lasiophyton*) *dregeana*; Z, *D.* (*Lasiophyton*) *hispida*. Components N to Z are of species with effective wings at one end of the seed, either directed towards the apex, components O and P or directed towards the base of the loculus.

in Q, R, S, and T. The rest are seeds winged towards the base. The capsules are shaped so as to hold the seeds after the seed-wings have grown. The wings, but not the nuclei, overlap. Sometimes this overlap is untidy, permitting as in J the two seeds to be unlike. Most of the capsules are reflexed as indicated; but the most effective gliders are not. It may have been that in early times seeds tended to be from basal to median on the placenta; then if so, seeds apical was the last evolution. Apical position suited best species with vigour but not competing in the deepest forests and is found in the Old World's commonest species as *D. bulbifera* and *D. pentaphylla*.

The wings must have been variable through early times; and a complete loss not unlikely to happen where Natural Selection did not give them use. So it happened that dwarf plants might lose them, as in *D. pyrenaica*, *D. perdicum* and some others. It might even be profitable to lose them if the wind tended to carry the seeds too far, as would appear possible in the case of both these species. Suppression of the wing could not happen in the high climbing species.

After the winged seed of *D. cochleari-apiculata* has had its adventure the wing is not wanted and there is an absciss ring on the margin of the nucleus which, getting wetted, lets nucleus and wing part company. The nucleus can then fall into any convenient crack in the soil. In *D. longicuspis* the wing may be seen acting as a shelter for the germinating seedling which under the direction of its positively geotropic radicle emerges downwards with, it may be, the wing of the seed between it and the wind.

This does not quite terminate the account of the seed-wing, for it remains to be said that in the American section Sarcocapsa and in the Madagascan section Campanuliflorae there are species with seed-wings small in proportion to the nucleus, as if in process of losing them; but further inquiry is desirable.

Of greater interest is the transfer of the wing from the seed to the capsule-wall in the genera *Avetra* and *Rajania*. As *Avetra* is a relict of the para-Dioscoreeae the transfer was remote; but the transfer in *Rajania* is going on today and it is hoped that attention may be drawn to the capsules of the growing plant. Our first knowledge came when Benjamin Lincoln Robinson gave the name *D. cyphocarpa* to a curious Mexican plant of the section Polyneuron, with only one of the three wings of the capsule allowed to grow. He did not describe it; that was left for Knuth to do in 1917, but he was unable to say whether two seeds are produced in the fertile loculus or one only. Robinson and Seaton had described in 1893 an allied species—*D. minima*—also from Mexico, but from a male plant, so that the interesting feature was not revealed. Pringle in Mexico also had in 1900 obtained specimens of another ally which Uline called *D. platycolpota*; but the capsule did not attract his attention. Latterly a fourth species has been described by Lunnell—*D. tacabensis* (*Lloydia*, **2**, 78, 1939)—who states that there is but one seed in the fruit. Is this fruit a samara, i.e. indehiscent; or is there a delayed dehiscence? The plants are manifestly intermediate between *Dioscorea* and *Rajania*; and it is interesting to see that the flower is dragged in growth to a horizontal position in the same way as on the fruit of *Rajania*. These Dioscoreas want no more than the suppression of dehiscence to make them *Rajania*. Few would doubt the origin of *Rajania* from *Dioscorea*; and here we see the latter still building up the former. Its organogenetic processes towards the end are open to laboratory studies and should be studied.

Corner has collected together (*J. Linn. Soc.* (*Bot.*), **56**, 36, 1958) some illustrations of transfer of function: this should be added to his list.

In *Avetra* the transfer of function gives to the one ovule that is not aborted means of reaching a greater size and for the propulsion by the wind it has the service of a greater surface. Perrier has described the samaras as needing the strength of a gale to tear them free, and states that if they are not torn free sometimes they germinate on the vine. This tearing free reminds one of the fruits of *Trichopus* being torn free by flood waters.

The size of the seeds of *Avetra* may be attributed to a benefit that must be to the seedling's good, which in evolution overcame the pressure towards lighter and lighter seeds for wider transport. Will the curious *Dioscorea-Rajania* transfer lead to larger seeds? *Avetra*, like *Stenomeris*, *Trichopus* and *Tamus*, is a very small genus of satellite rank.

The fruit-wall needs viewing from two points: the one follows its growth of the loculi to capacity; the other its shaping for usefulness in the dispersal of the seeds. Growth to capacity means enlargement of the loculus to accommodate the flattened seeds and their wings. It is based on elongation being greater in the three interseptal bundles than the group of bundles in the placenta; with this greater elongation they become arcuate, seeming to trail after them the soft tissues between them and the placenta, whose cells accommodatingly elongate in the direction of the pull. The stimulus for this growing comes from the direction of the placenta and leaves the wall thinnest close against the arcuate bundles. That thinness is preparation for dehiscence. There is also a decrease in strength towards the apex of the fruit which determines that the dehiscence shall commence distally. The dehiscence when it comes is purely mechanical. Sometimes it leaves the margin looking like a bit of wire by occurring on both sides of it; sometimes it does not. The interior of the wall becomes perfectly smooth. In those Dioscoreas whose seeds are jerked free, preparation for this begins immediately after fertilization by the entry of negative geotropism into the short stalk under the ovary; and the rudimentary capsule is turned upwards. Growth here and of the margin is clearly activated from fertilization; what happens is the holding back of two loculi to make possible the samara of the section Polyneuron.

The time for the capsule walls to dry is not invariably among the Dioscoreas the time when the seeds attain full age. In the Madagascan *D. ovinala* the capsule walls retain moisture for a further 6 months (Perrier de la Bâthie), and in the American section Sarcocapsa for a period not yet measured. *Tamus*, assuredly derived from *Dioscorea*, has no dehiscence and under a protecting roof the berries may be kept all winter in a fleshy state. There is much peculiar in the reproduction of the last-named. The fruit-wall is from its beginning fleshy and the parenchyma which constitutes it, is a water-store for the growing ovules. At fruit-ripeness this parenchyma partly degenerates into a mucilaginous fluid which has the property of inhibiting the germination of mustard seed. It has not been tested with other seeds (*Proc. Linn. Soc. Lond.* **169**, 62, 1958). What its part may be is not clear for the seed of *Tamus* has a very long after-ripening and undergoes it whether in the fluid or removed from the fluid. It needs moisture and seems to get it while in the fluid, but this is never for more than a part of the after-ripening.

There is parallel evolution in the delayed drying of the two Dioscoreas and *Tamus*. There may be slight zygomorphy in the reflexed capsules of a few species; by it one wing of the capsule is a little less prominent towards the pedicel than the others (see figures in the *Flora Malesiana*, 301, Fig. 5 K–N). It is likely that the one loculus which is allowed to grow in such species as *D. cyphocarpa* and in the genus *Rajania* is pre-determined: is it entangled with the geotropic reversal of the pollinated ovary? The slight zygomorphy to be seen in the stigma of *D. sylvatica* may be recalled (for a description of it see *J. Bot.* **1940**, 100).

To complete what needs to be said regarding the fruit-walls, the curious accessory vascular bundles of the species of the section Borderea and the curious frill of the Madagascan *D. acuminata* need mention. The vascular bundles mentioned are readily seen in *D. pyrenaica* and *D. gillettii*. They arise from the arcuate marginal bundles of the capsule wings and run towards the apical half of the placenta, where they break up. The frills of *D. acuminata* are epidermal ridges of uncertain appearing and as yet are not explicable. They were the cause of that species receiving the name '*D. fimbriata*'.

The seed of *Tamus* having reached the soil, buries itself by alternate swelling and drying, swelling when water reaches it, expanding its bed, drying and shrinking, then getting wet again and expanding again. This leads to it being several centimetres down when after-ripening is over. No other part of the family does exactly the same; but *D. humilis* tries to bury its subglobose fruit whole by pressing it down on a spiral pedicel, but there must be a breaking up of the fruit which as yet has not been described. The seeds appear to germinate more promptly than the seeds of *Tamus*. Miss P. Smith experienced some difficulty in germinating *D. villosa* (probably its segregate *D. glauca*), but did not explore further (see her paper in *Bull. Torrey Bot. Cl.* **43**, 547, 1916).

Fig. 57 illustrates the seed in transverse section. Components A, B, C and D are flattened seeds; E is the round seed of *Tamus communis*. The endosperm, except in *Tamus*, has a median parting. A is through the nucleus of *D. bulbifera* above the wing, B, C and D are of the wingless seeds of other species. Brenner has described the cellular structure of the seed-coats of *Tamus* and the reader is referred to his work (in Kirchner and others, *Lebensgesch. Blütenpfl. Mitt. Eur.* **1/3**, 691 ,1914), and also to Marloth (*Bot. Jb.* **4**, 225) and to Gardiner and Hill on the nature of the endosperm of *Tamus* (*Proc. Camb. Phil. Soc.* **11**, 445, 1902). But as yet no comparative examinations have been made to which a taxonomist can turn.

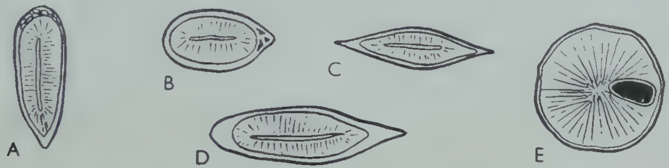

Fig. 57. Seeds of *Dioscorea* in transverse section, × 5. A, that of *D. bulbifera* at a horizon above its wings, showing the split endosperm; B, C and D, three wingless species, *D. pyrenaica* sub.sp. *D. chouardii*, *D. gillettii* and *D. perdicum*, showing to what the wings are reduced and that the endosperm is split. E, The spherical seed of *Tamus communis* cut on the radius of the embryo showing that there is no split in its endosperm. The endosperm cells being in lines reflect light in lines.

§38. *Chromosomes*

Observations on chromosomes are increasing in number and in interest. It is apparent that the section Stenophora is characterized by $2n = 20$. *D. pyrenaica* of the section Borderea has $2n = 24$ and *Tamus* has twice that, which is a fact supporting the belief that *Tamus* is related to that part of *Dioscorea* wherein is the section *Borderea*. A wide range of tropical Dioscoreas have $2n = 40$, which is twice that of the Stenophoras. It is gradually becoming evident that the basic type for *Dioscorea* is 10. In a paper newly published (*Proc. Indian Acad. Sci.* **48**, 59, 1958) Sundara Raghavan records $2n = 40$ for seven species which occur in India (including one species of the section Stenophora—*D. deltoidea*) and other multiples of 10 ($2n = 20$) for four of them.

High numbers are met with in the species which Man uses in particular for food, in a way that stresses the connexion between cultivation and polyploidy.

A paper on the nucleus of *Dioscorea* by Professor J. Miège (*Rev. Cytol.* **15**, 327, 1954) may be consulted with profit.

IV. CONCLUSION

I come to the task of suggesting a sequence by which the Dioscoreaceae may be arranged to advantage when codifying information regarding the family. As to genera the task is not difficult; but as to sections of the big genus *Dioscorea* it bristles with difficulties. I take the genera first, and give a key as a convenient way of getting them into perspective. The sections of *Dioscorea* follow at p. 402.

Key to the genera of the Dioscoreaceae

(The family emerged out of the proto-Liliales as tropophytic, perennial herbs with a rhizome and broad leaves, and with hermaphrodite flowers having the formula K_3, C_3, A_{3+3}, $\overline{G}_3$)

1. Stem self-supporting. Ancestors in the Liliaceae–Asparagoideae

1′. Stem becoming upwards unable to support itself and then twining. (This was the first birth of the Dioscoreaceae.) proto-Dioscoreaceae

  2. Sexes united in the flower; rhizome thin. (The few extant species do not have winged seeds and are dependent on great humidity; the lost species must have had winged seeds.) para-Dioscoreeae

    3. Two ovules in each loculus.

      4. Fruit a samara, with 5 of the 6 ovules aborted, the remaining seed wingless. (Stem tall enough to twine.) *Avetra*

      4′. Fruit a berry. (The plant too dwarfed to climb; seed wingless.) *Trichopus*

    3′. Numerous ovules, followed by winged seeds. (Wing of seed directed forwards; stem climbs.) *Stenomeris*

  2′. Sexes in different plants; a thickened rhizome in some species, otherwise a tuber. (The storage organ, in any case with greater storage capacity, and the increased amount of water held enabling growth when atmospheric water is in short supply. This gave rise to the second birth of the Dioscoreaceae.) proto-Dioscoreeae

    5. Fruit a berry; female flower not unlike the male. *Tamus*

    5′. Fruit dry, wind-dispersed; female flower tending to be unlike the male

      6. Fruit a capsule. *Dioscorea*

      6′. Fruit a samara. *Rajania*

It is profitable to construct from this key a diagram in pedigree-form with the small genera as satellites to the large genus *Dioscorea*. The satellites which emerged in the Old World are placed on the right; and the single satellite which emerged in the New World is placed on the left.

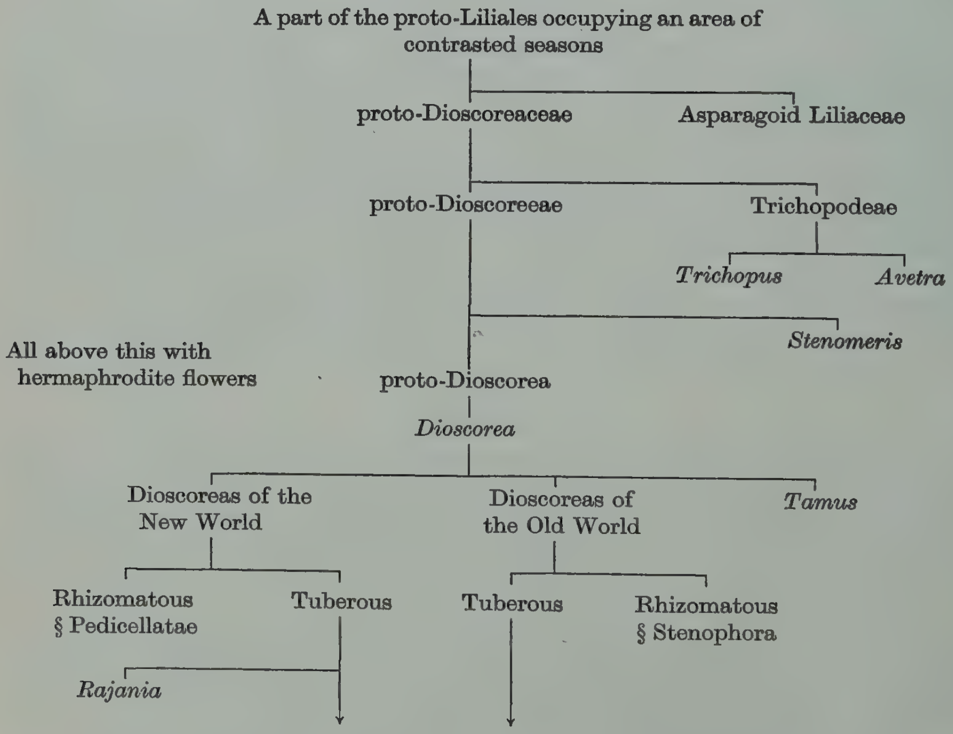

Fig. 58. *Dioscorea* and its satellite genera.

Eastern origin of the family

The excess of satellite genera on the right over that on the left is attributable to the family having had a longer history in the Old than in the New World—which postulate has the support of: (i) the circumstance that the Taccaceae and Stemonaceae, being the families of closest alliance to the Dioscoreaceae, are predominantly eastern; (ii) the genera of the Asparagoideae of closest affinity such as *Paris* and *Aspidistra* (*Tupistra* may be taken with *Aspidistra*), are also predominantly eastern; (iii) the para-Dioscoreeae of the *Nepenthes* Arc are eastern; and on the other side (iv) *Rajania* is certainly of very late origin.

The para-Dioscoreeae a side show

The *Nepenthes* Arc curves over a part of the Globe which formerly was Gondwana Land; and there is nothing against believing that the deluge plants of the Arc are survivors from a Gondwana-Land Flora. Gondwana Land broke up in the end of the Cretaceous in tremendous cataclysms which spread enormous sheets of lava in India and sent extensive land-surfaces to the bottom of the sea. The points of land today projecting. southwards are deluge areas; and their most peculiar plants are deluge plants. As there is no reason which can be adduced against the blowing of an 'Indian Rainy monsoon' over Gondwana Land, the para-Dioscoreeae appear as relicts from a climate which that monsoon produced; then furthermore, as these relicts are morphologically very divergent, they are fragments of a network lost along with Gondwana Land. With the Trichopodeae should be associated *Stenomeris*. The student of geological climates will note the evidence of deluges that the plants supply; and the student of phyto-geography must recognize that the specialization of the plants implies that they were not in the real line of the advance of the Dioscoreaceae, but existed as a side-issue suited to conditions confined within eastern parts of the World. Elsewhere, under conditions of less tyrannous humidity, the proto-Dioscoreeae were coming forward parallel to the para-Dioscoreeae, and were denizens of tropophytic climates whose wider extent over the globe was inviting their ability to spread. Put succinctly, I understand the Dioscoreaceae to have been of eastern origin but as having established themselves towards the west so widely, and early enough to be considerably affected by the Atlantic Rift when it divided South Africa from South America. The establishment in Africa thus had a large part in forwarding the success of the family.

Mystery in the introduction of dioecism

It is curious and intriguing that the unsuccessful para-Dioscoreeae should have kept the ancestral hermaphrodite condition, but the successful Dioscoreeae should have become dioecious—intriguing because sex-separation would make difficulties in pollination. That the proto-Dioscoreeae succeeded is obvious; and that their superior ability to live was in some other quality.

Under headings (3) (p. 323) and (4) (p. 325) I have tried to collect reasons for ascribing the success to water-supply adaptations, and to show that dioecism in the Dioscoreeae, though a tremendous evolutionary jump, probably took off from a stock with cross-pollination devices of which it was an intensification. But the course of evolution in this respect is difficult to envisage.

Sex-separation carried with it a reduction in the size of the flower and in the sexes a divergence which ultimately reduced the female flower to an alighting platform, leaving the male an attracting organization. Of the many guesses that botanists have made on the life of Dioscoreaceae none has less substance in it than that the flowers are anemophilous.

True it is that there is no need for wind-fertilized flowers to exhibit any resemblance between the flowers of the two sexes and everyone knows how greatly they differ: but if the flower-visiting insects be blind or more or less blind there is equally no reason for the flowers of the two sexes to be alike; and the case seems to be that crepuscular or nocturnal pollination has been overtaking the diurnal pollination which the family had at first. When *Tamus* arose out of *Dioscorea* the dissimilarity of the flowers of the two sexes had not gone far; and *Tamus communis* is fertilized in Britain and the Swiss Alps (and doubtless elsewhere) by day-flying sight-guided insects (see p. 393); but the tropical Dioscoreas in a large measure seem to be pollinated at night by agents which reach the flowers guided by scent. It could, furthermore, be that in contact with the flowers they feel a warmth that helps to guide them—the same warmth that fills the spathe of various Aroids with small flies.

I would digress here for a moment to ask why the sexes were parted—did the flowers lose size? As the loss of size occurs, for instance, in the Labiatae when the normally bisexual flower loses its functional stamens, so, too, to the loss of the male sex in the Dioscoreaceae can be attributed a lessening of conspicuousness of the flower, without invoking insect vision.

As to the entry of sex separation into the Dioscoreaceae its occurrence in *Asparagus*, *Smilax*, and a few other Liliaceae suggests that comparative studies might give a little light. It is a circumstance that these Liliaceae are climbers as are the Dioscoreaceae: but what is there to connect sex-separation with their habitat or way of life?

The first Dioscoreas

I would now attempt to visualize the earliest Dioscoreas. They must have had sex separation though with little differentiation in the flower. Undoubtedly they twined, and the stems carried from low down entire, auricled, long-petioled, gland-tipped leaves; for these characters existed before their time and were passed forward by them. They were dispersed by winged seeds released from parchmenty capsules and there would be two seeds in each of the three loculi. Underground the transformation of the rhizome into a tuber would be in various stages. The fact that *Avetra* twines to the right suggests that the direction of twining might be in either direction, though chiefly to the left. Just as there was a progressing advance underground whereby the storage grew increasingly efficient, so there would seem to have been a running change within the capsules whereby the position of the seeds on the placenta was moved upwards, as it is beyond dispute that the most efficient gliding seeds need growth upwards and downwards and the most efficient whirling seeds need all their growth downwards.

The majority of the species within proto-Dioscorea would be glabrous.

Dioscorea's Old World expansion

I proceed to the arrangement of the Old World sections of the genus *Dioscorea*, all of which, of course, came out of proto-Dioscorea. It is convenient to begin with a key, the first characters of which must be based on the storage organs and a high place be given to the seeds.

A key to the Old World sections of the genus Dioscorea[1]

1. Storage in a rhizome. Stenophora
1′. Storage in a tuber.
  2. Annual increment within the tuber from a continuous growth zone which increases the size of the tuber without altering its shape.

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[1] The South African species, *D. brownii* Schinz, *D. burchellii* Baker and *D. stipulosa* Uline have not been accounted for in the above key, as new material is being sought for their adequate placing.

3. Dwarfed plants of rocky places; wingless seeds. (Tuber with a rather thin layer of cork.) Borderea

3′. Rather small, but not dwarfed, climbing; seeds winged. (Tuber with a very thick coat of cork, so hard that above the soil no other protection is needed.) Testudinaria

2′. Annual increment to the tuber not covering the surface of the previous year.

4. Annually new storage swelling crowns that of the previous year. (A high climber with intensely poisonous tubers which are at the surface of the soil, and have no corky coat.) Macroura

4′. Annually storage lobes are directed downwards, depleted for the growth of the next year and replaced.

5. Perennial bud on the tuber so close to the surface of the soil that the annual stem comes above the soil in its first internode.

6. Torus of the male flower virtually absent. (Annual lobe thick-necked, single, broadly attached to the corm.) Opsophyton

6′. Torus of the male flower enlarged as the top of the pedicel. (Lobes of various forms.)

7. Seeds winged for gliding, i.e. the wing is disposed to balance the seed in flight.

8. Male inflorescence a simple spike or if the flowers are pedicellate the pedicels so short that it is spiciform; sometimes a second flower is present on the pedicel of a few of the lowest flowers.

9. Stem twining to the right.

10. Male flowers as little water-stores, all as a rule closely packed: hairs stiletto or dendroid, but not stellate. Enantiophyllum

10′. Male flowers herbaceous; hairs stellate. (Anthers sometimes apiculate.) Asterotricha

9′. Stem twining to the left; male flowers strictly racemose.

11. Seeds evenly winged all round. Stenocorea

11′. Seeds with equal wings extended from either end. (Laminae very generally lobed.) Rhacodophyllum

8′. Male flowers in small cymes along a racemose axis.

12. Seeds as in the last section with even wings extended from either end of the seed. (Strangely hooked hairs.) Macrocarpaea

12′. Seeds evenly winged all round.

13. Leaves very variable, if large lobed or compounded; fertile stamens 6. Cardiocapsa

13′. Leaves entire; fertile stamens 3. Madagascarienses

7′. Seeds winged for whirling before a puff of wind, incapable of gliding, the wing being entirely or almost entirely from one end of the seed.

14. Wing directed towards the distal end of the loculus; laminae simple, entire.

15. Stem twining to the left.

16. Capsule 4–6 times as long as broad; seeds with wings as in the genus *Stenomeris*, being fan-like. (Tuber may carry thorny roots.) Paramecocarpa

16′. Capsule about twice as long as broad; seeds with or without the wing extended down the margin.

17. Corm giving origin to numerous clavate lobes lying under a fierce armature of thorny roots; or in cultivated races unarmed; male inflorescence spicate; ability to fruit almost lost. Combilium

17′. Corm giving origin to a single annual tuber; male inflorescence with little cymes of flowers along its axis. Shannicorea

15′. Stem twining to the right. (Male flowers on a raceme on very short pedicels; capsules with high shoulders.) Cotonifoliae

14′. Wing directed towards the base of the loculus; laminae compounded.

18. Male flowers with no pedicel, but if not sessile then raised on a pediment which lifts the bract of the flower with the flower; capsules sometimes too large and heavy to become reflexed completely; fertile stamens often reduced to 3. Lasiophyton

18′. Male flowers at the base of the inflorescence in small cymes, but there only: stamens of two sizes. Illigerastrum

5′. Corm deep enough in the soil for 2–3 internodes to be within the soil. (The margins of the seed usually carry traces of the wing, which is directed towards the base of the capsule.)

19. Capsule-wall woody. Xylinocapsa

19′. Capsule-wall parchmenty at the end of the season's growth.

20. Male flower-bud globose.

21′. Torus of the male flower making a bell at the mouth of which the 6 anthers stand, their filaments inserted at the very base. Campanuliflorae

21′. Torus of the male flower cup- or saucer-shaped; stamens inserted just above the base. Brachyandra

20′. Male flower-bud pyriform (inflorescence a raceme). Seriflorae

19″. Capsule-walls retain their fleshiness as in *Tamus* beyond seed-ripening for upwards of 6 months. Pachycapsa

The twenty-three sections, keyed above, are scattered in the following diagram by their apparent relationships (Fig. 59). If the relationship is regarded as very close the circles touch; otherwise they are placed appropriately apart. Down the centre of the diagram a line divides the African from the Asian sections. The three sections that are in both continents are on that line. The sections which preserve characters regarded as having been brought forward from proto-Dioscorea, are at the top of the diagram. Stenophora, with rhizomes, is there; Paramecocarpa, with seeds like those of *Stenomeris* and with elongated capsules, is there; both are Asiatic. On the African side of the line, with a common sign to connect them, are the sections Borderea, Testudinaria and Macroura which have a tuber with an embracing growth-zone—partial in Macroura, general in the others. Madagascar's two contingents, the one characterized by a deeply buried corm (D) and the other made up of Cardiocapsa and Madagascarienses, are towards the left lower corner; in the last two the ovules are medial on the placenta so that there is space for the seed-wing to surround the seed which glides away from the capsule when freed. These are marked M (mid-placenta). M is also on the circles for Asterotricha, Enantiophyllum and Stenocorea; all five are together in the lower part of the diagram. In contrast, the mark ∞ means seeds able to glide by the equal size of the wings at either end of the nucleus; X indicates wings limited entirely to the lower side of the seed which, for the accommodation of the wings, must be placed high on the placenta. Like the X group, the D group has seeds placed high on the placenta, but the wings are narrowly continued down the ridge of the seed, as if they might be X in an imperfect state. The suggestion that this leads to, is that Madagascar received the ancestry of the D group with the seeds in transition. A consequent postulate is that Madagascar received the ancestry of Cardiocapsa at a different time and in a different way from the coming of the ancestry of the D group. In whatever way we look at the Madagascan Dioscoreas it seems plain that the island received two lines—the D line and the Cardiocapsa line. R indicates twining to the right and *C* indicates having compound leaves. One of the sections—Cotinifoliae—which twines to the right is very distant from the other two. I have dealt with left and right twining on p. 343, showing the direction sometimes, apparently, quite accidentally is reversed; and I have pointed out on p. 379 that compounding of the leaves must have appeared in the family on different occasions: I count therefore that the marks *R* and *C* should not be thought misplaced if dispersed because ranked of lower value than those discussed before them. But it is natural to be surprised that the pulvinus, so deeply entrenched in the family, should be broken into at all.

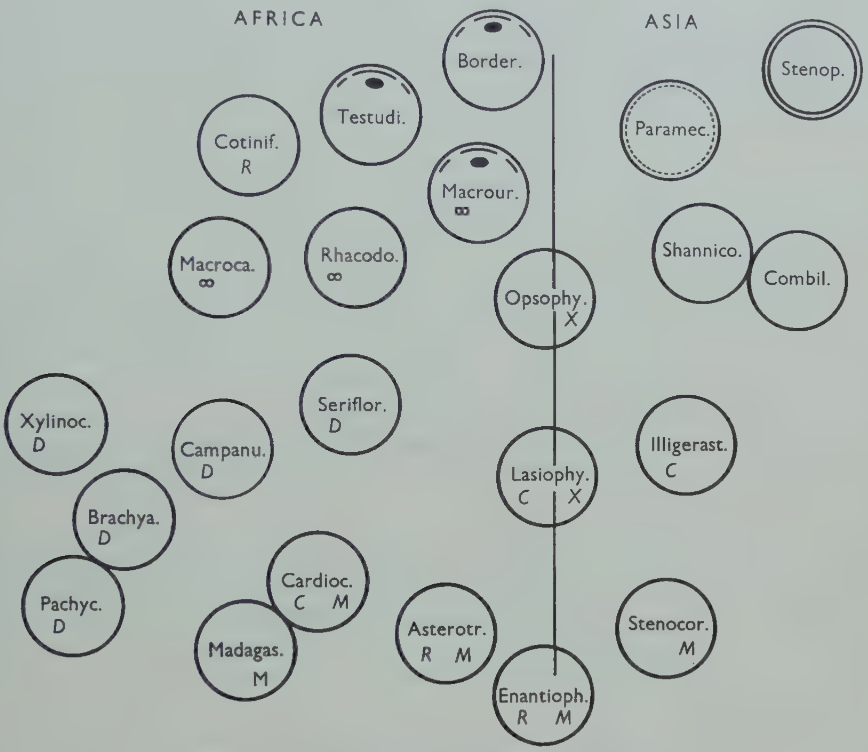

Fig. 59. Relationship of sections of *Dioscorea*.

Sectional successes

The largest of the sections are Enantiophyllum and Lasiophyton. I am inclined to attribute this to speciation to the eastward of India after the Miocene. I would draw the reader's attention to Merrill's *Enumeration of the Philippine Flowering Plants* (**4**, 61, 1926) where, having said that the generic endemism of the archipelago is remarkably low, he continues crediting approximately 7620 species to the Archipelago: 'Of these no less than 5832 or about 76·5 % are known only from the Philippines' and 'we may conclude then that the Archipelago as a whole has been separated geologically from neighbouring islands for a sufficiently long period to allow for the development of a remarkably high percentage in specific endemism, but not long enough to allow for the development of many distinctive genera'. Enantiophyllum, having a wide distribution in the East after the Miocene climatic continuum had cut it into western and eastern parts, profited in the Philippine flora by opportunities for speciation and became large. And perhaps Lasiophyton profited in the same way. But obviously there may be sections attuned and sections not attuned to the conditions; one such would be Paramecocarpa which remained very small. Its characters suggest that it is older than Enantiophyllum. Its distribution suggests a demand for considerable humidity.

The more search that is made for the origin of the sections of *Dioscorea* the more does it seem that every section originated before the Miocene, but almost every species from the Miocene forward.

Opsophyton is a peculiar section. Small in the number of its species, its *D. bulbifera* is very outstanding in the construction of its male flowers; it is very fertile both sexually and asexually, small-seeded, but the seeds efficiently shaped, and it is in its haste to reproduce somewhat precocious. The plant in Africa and the plant in Asia are diverging, the African plant producing small finger-like hairs, but in such small numbers that they would seem to be quite outside the influence of natural selection. The chromosome numbers so far recorded disclosed an unco-ordinated range. It is the only extant species demonstrably existent in the Miocene.

Dwarfing as a sectional character

There are numerous dwarf Dioscoreas in the New World and few in the Old; so that we have to ask ourselves not only what caused them, but why the result is large in one continent and small elsewhere.

The great home of the dwarfs is the Pacific slopes of the Andes. As seedlings and young plants they take there the shelter that they require from rocks instead of trees and in the absence of tree-cover find themselves without the compelling urge to climb. Long ages of little varying climate have enabled not inconsiderable sections to be built up on a thrift by which they live under poor conditions.

Dwarfs, not quite so pronounced as those of the Andes, extend northwards to Mexico, and are doubtless of parallel origin; and it must be that the section Borderea of the Mediterranean is also parallel.

If the conditions on the Pacific slopes of the Andes were to be made more severe, the dwarf Dioscoreas there would be open to killing out; if the conditions became good enough for trees, they would be smothered out. On either side of them is a threat; and the first of the two threats would be that which has almost destroyed Borderea. The state of Borderea illustrates the state of Testudinaria; but Testudinaria has not been pushed so far towards dwarfing as Borderea, nor tried so severely. Whether at any time this kind of dwarfing occurred in Asia is not evident, for there are no rock-sheltering Dioscoreas known in Asia.

The spreading of a section into open savannah is a different process. It is particularly evident in Africa, where *D. quartiniana* is by no means excluded from growth among 2 m. high grasses. The extreme is reached in Madagascar where *D. hexagona* grows in grassy stretches down to a size of 30 cm. Should it happen to grow on their edge in soil good enough to support a bush the stem-tips twine on a branch if they reach one; otherwise they stand strictly upright; below the top the leaves have unduly short petioles (see p. 378), and the auricles may be entirely absent, the lamina narrowing into the petiole. The nearest ally to *D. hexagona* is *D. soso* which grows in open forest, and twines freely.

Savannah in southern Brazil is the home of *D. campestris*—a species equally with narrow laminae and of some others that are similar.

The phyto-geographer may reasonably hold that the genus *Dioscorea* has from its beginning been liable to slip into a dwarf condition; but nothing that we know enables one to understand the manner in which *Trichopus* came to be a dwarf.

Some desirable inquiries

It had been my wish to get an idea of the morphological condition of *Dioscorea* at the end of the Cretaceous by comparing the sections of Africa and America; but I have not had enough of the American species in cultivation. The comparison is expected to show that the proportion of species with a continuous growth zone in the tuber is higher in the New World than in the Old, and to expose the magnitude of the contrast in size of the male flowers between species of South America and Asia. Attention may be called to Karl Reiche's claim that Epipetrum has a growth zone in its tuber (see *Bot. Jb.* **42**, 181, 1908).

When these morphological comparisons are instituted the comparison should be extended to the protective animal poisons. Saponins are general in the Old World and it is apparent that they have by no means seldom been called alkaloids. That one species of the section Enantiophyllum should provide a tanning material (*D. cirrhosa*) is worth further inquiry.

Even in the service of Man there are East and West differences. The East has produced the most useful yams—*D. alata* and *D. esculenta*—and has given them to Africa and to the New World; Africa has produced *D. rotundata* and *D. cayenensis* and has given both to the New World, but neither to Asia; the best that the New World has produced is *D. trifida* which has obtained a very little attention in the very north of Ceylon, but not elsewhere in the East. Three out of these six belong to the section Enantiophyllum: it is therefore because initially this section belongs to the Old World, that the Old World has been able to give without return. But that drives us to another question—what led the Old World to a pre-eminent evolution of deep-burial of tubers as opposed to poison as a protection? Therewith, and long before Man's interference, the Dioscoreas of the East were being shaped towards his later advantage. Then with some such weapon as a deer's antler in his hand, Man readily turned the defence of prickles or thorns, entered into a struggle with the soil and took what he could uncover. This food-gatherer was merely destructive; and it was not he who commenced cultivation. Tillage, indeed, does not begin with such as he, but among men who have a more secure source of food. I attribute the first cultivation of yams to fisher folk. The first tilling of Asia must have been that of south-western Asia where Dioscoreas do not grow. Far from this, and quite independently, dwellers on the banks of the rivers of south-eastern Asia and of the coasts whose food consisted largely of fish, originated another cultivation and it was into this that *Dioscorea* entered. The river's spill or a beach thrown up by the sea provided the place for their houses. Behind this mound or raised beach they sheltered their boats; and a backwater where the forest growth was made thin by the wet soil and its muddy approaches gave an area within which it was easy to plant *Colocasia* and other aroids. Success with *Colocasia* led to the bringing of Discoreas to the drier margins. This new tillage eventually brought in rice, first as broadcast, then at a very much later period behind dams that held up water. If I am right in regard to Asia a like tillage began on the Guinea Coast of Africa which in a similar manner accepted *Dioscorea*—primarily *D. cayenensis* and when extending inland *D. rotundata*.

A curious condition is found in *D. esculenta*. Food-gathering man seems to have exploited it so intensely that it is rare as a wild plant. That Man when he had learned to till, selected away its fierce thorns is apparent, but in his hands it became sterile, with a sterility that would inhibit further selection against thorniness. But by what way did the sterility come? The sterility inhibited flowering in the female, but the male plant in some races produces male flowers plentifully. These circumstances seem to offer interesting studies. As a field crop *D. esculenta* usually has its harvest taken too soon for flowering, and the replanting throws it back year by year.

D. alata as a field crop gets the same treatment; but is more often left for a series of years and may reach flowering and produce seeds. The African allies flower and fruit freely.

Fifty-eight years have passed since by accident it fell to me to study *Dioscorea* in life. The material wanted has often come to hand very slowly; and there is much that I have tried in vain to get. In publishing what I now know I am moved much more by the hope of interesting others than by anything else. My debts to others are extensive. Latterly I have been helped considerably from Kew; but the tropical botanical gardens are the most favourable places for study, and this I trust will be appreciated. But a garden without a laboratory is inadequate. There are a few fellow workers to whom I am particularly indebted and very grateful:—the late Prof. Auguste Chevalier for much information over many years on African Dioscoreas, Mr C. G. Codd for cultivating South African species, Dr C. R. Metcalfe for help in laboratory work, Prof. J. Miège for his Guinea studies, Mr E. Milne-Redhead for collaboration at Kew, the late Major M. Y. Orr for undertaking studies of the glands, M. H. Perrier de la Bâthie for his work on Madagascan species and his readiness to collaborate with me, Dr Bernice G. Schubert for information collected in North and Central America and Mr E. V. Watson for his work on *Trichopus*. These are but a few among many. Mr F. Richardson's skill in microscopic technique has been of much service.

LIST OF THE SPECIES USED IN ILLUSTRATION

Dioscorea (Enantiophyllum) **abyssinica** Hochst. From Abyssinia southwards.
D. aculeata L. in 1754 (not in 1753) = *D. esculenta*.
D. (Campanuliflorae) **acuminata** Baker. Deciduous forests of West Madagascar.
D. (Dematostemon) **adenocarpa** Mart. South Brazil and Paraguay.
D. (Enantiophyllum) **alata** L. The Greater Yam; origin in tropical eastern Asia, now pantropic in cultivation.
D. (Strutantha) **amarantoides** Presl. Warmer parts of South America whence brought into horticulture.
D. (Brachyandra) **analalavensis** Jum. & Perr. Deciduous forests of West Madagascar.
D. (Dematostemon) **anomala** Griseb. In savannahs in south central Brazil.
D. apiculata De Wild. = *D. quartiniana*.
D. (Xylinocapsa) **antaly** Jum. & Perr. Hills of West Madagascar.
D. (Lasiophyton) **arachidna** Pr. & Burk. Indo-China.
D. (Madagascarienses) **arcuatinervis** Hochreut. East Madagascar.
D. (Stenophora) **balcanica** Kosanin. Edges of forests in Albania.
D. (Cryptantha) **bartlettii** Morton. Central America. A close ally of *D. polygonoides*.
D. batatas Decne. = *D. opposita*.
D. (Enantiophyllum) **baya** De Wild. A large species of the Congo forests.
D. (Brachyandra) **bemandry** Jum. & Perr. Deciduous forests of West Madagascar.
D. (Stenophora) **birmanica** Pr. & Burk. A rather large species of Burma.
D. (Stenophora) **biserialis** Pr. & Burk. South-west China.
D. (Enantiophyllum) **brevipetiolata** Pr. & Burk. Indo-China and Malaya.
D. (Chirophyllum) **bryoniifolia** Poepp. Andes of Chile.
D. (Rhacodophyllum) **buchanani** Benth. South-central Africa.
D. (Opsophyton) **bulbifera** L. Tropics of the Old World, in various parts of which it has given cultigens; now also in the New World.
D. (Dematostemon) **bulbotricha** Hand.-Mazz. South Brazil.
D. (Enantiophyllum) **burkilliana** Miège. West Africa in the wetter parts of Guinea.
D. (Dematostemon) **campestris** Griseb. South Brazil and Argentine.
D. (Stenophora) **caucasica** Lipsky. Between the Caucasus and the Black Sea.
D. (Enantiophyllum) **cayenensis** Lamk. Wild and cultivated in Guinea and transported to tropical America.
D. (Stenophora) **chingii** Pr. & Burk. South China.
D. (Borderea) **chouardii** Gaussen. A subspecies of *D. pyrenaica*.

D. (Enantiophyllum) **cirrhosa** Lour. Southern China and Indo-China, peculiar in the amount of tannin which it carries.

D. (Lasiophyton) **cochleari-apiculata** De Wild. A large species of east tropical Africa.

D. (Stenophora) **collettii** Hook. f. Widely in China.

D. (Brachyandra) **comorensis** R. Knuth. Comoro Islands.

D. (Trigonobasis) **convolvulacea** Cham. & Schlecht. Widely in Central America and reported as in Africa (introduced).

D. (Monadelpha) **coronata** Hauman. Argentine.

D. cretacea Lesq. an unsatisfactory name for a fossil from the Cretaceous deposits of North America.

D. (Trifoliatae) **crotalariifolia** Uline. Tropical America.

D. (Lasiophyton) **crinita** Hook. f. Subtropical South Africa.

D. (Polyneuron) **cyphocarpa** Robins. Mexico.

D. (Stenocorea) **daunaea** Pr. & Burk. Of scrub and forest margins in Indo-China.

D. decaisneana Carrière, a form of *D. opposita*.

D. (Stenophora) **deltoidea** Wall. In the Himalaya and eastwards to Tonkin.

D. discolor Kunth, a clone or clones of cultivated *D. dodecaneura*.

D. (Rhacodophyllum) **diversifolia** Kunth. South Africa.

D. (Lasiogyne) **dodecaneura** Vell. A vigorous and widespread species of South America, a pre-hispanic food and and a source of horticultural clones.

D. (Lasiophyton) **dregeana** Th. Dur. South Africa.

D. (Lasiophyton) **dumetorum** Kunth. Very widespread in tropical Africa and a source of cultivated races.

D. eburnea, an erroneous name used by Goebel for the clone '*D. discolor*' of *D. dodecaneura*.

D. (Testudinaria) **elephantipes** Engl. The well-known Elephant's foot of South Africa.

D. (Monadelpha) **entomophila** Hauman. Argentine.

D. (Combilium) **esculenta** Burk. The legitimate name for Loureiro's *Oncus esculentus*. Indo-China whence into cultivation in the East and distributed thence.

D. excisa R. Knuth, a variety of *D. quartiniana*.

D. fasciculata Roxb. A name covering the more selected cultigens derived from *D. esculenta*.

D. (Paramecocarpa) **flabellifolia** Pr. & Burk. A vigorous species of eastern Malaysia.

D. (Borderea) **gillettii** Milne-Redh. Kenya, towards Abyssinia.

D. (Monadelpha) **gaumeri** R. Knuth. The male of *Higinbothamia synandra* and probably the female. Central America.

D. (Enantiophyllum) **glabra** Roxb. The most frequent species of its section in India and Indo-China.

D. (Stenophora) **glauca** Mühl. Eastern United States, brought into gardens in Europe as '*D. villosa*'.

D. (Stenophora) **gracillima** Miq. Japan and north-east China.

D. (Enantiophyllum) **hastifolia** Nees. A species which has become isolated in west Australia.

D. (Testudinaria) **hemicrypta** Burk. A close ally of *D. elephantipes*. South Africa.

D. (Brachyandra) **hexagona** Baker. Grassy savannahs of central Madagascar.

D. hirsuta Dennst. = *D. hispida*.

D. hirsuticaulis Bartlett = *D. glauca*.

D. (Asterotricha) **hirtiflora** Benth. Widely in tropical Africa, tending to invade savannah.

D. (Lasiophyton) **hispida** Dennst. The legtimate name for what is variously called *D. daemona*, *D. hirsuta*, *D. triphylla*, etc. Wide in tropical Asia.

D. holstii Harms. = *D. quartiniana*.

D. (Microdioscorea) **humifusa** Poepp. A dwarf of the Chilean Andes.

D. (Epipetrum) **humilis** Bert. Lower Andes of Chile; the foundation of Philippi's genus *Epipetrum*.

D. (Stenophora) **hypoglauca** Palibin. Eastern China. Perhaps identical with *D. collettii*.

D. illustrata Linden & André, a clone(?) of *D. dodecaneura*.

D. (?Opsophyton) **inopinata** Pr. & Burk. Siam.

D. (Enantiophyllum) **japonica** Thunb. Japan and China.

D. javanica, a name used by Queva for *D. alata*.

D. (Lasiophyton) **kamoonensis** Kunth. Himalaya and eastward to Anam.

D. (Enantiophyllum) **kingii** R. Knuth. A vigorous species of Malaya.

D. kita Queva is not identifiable.

D. (Lasiophyton) **knuthiana** De Wild. Congo.

D. (Cycladenium) **kuntzei** Uline. Bolivia.

D. (Monadelpha) **lagoa-santa** Uline. Widely in South America.

D. (Enantiophyllum) **lamprocaula** Pr. & Burk. Western Malaysia.

D. (Enantiophyllum) **laurifolia** Wall. Western Malaysia, chiefly montane.

D. (Cryptantha) **laxiflora** Mart. Brazil.

D. (Paramecocarpa) **ledermannii** R. Knuth. Palao Islands, not yet clearly differentiated from *D. flabellifolia*.

D. (Cycladenium) **lehmannii** Uline. Colombia.

D. (Enantiophyllum) **liebrechtsiana** De Wild. A species of west tropical Africa not yet precisely known.

D. (Asterotricha) **longicuspis** R. Knuth. East tropical Africa.

D. (Cycladenium) **lundii** Uline. South-east Brazil.

D. (Enantiophyllum) **luzonensis** Schauer. Philippine Islands.

D. (presumed Stenophora) **lyelli** Wat. An Eocene fossil species of western Europe.

D. (Cycladenium) **macrantha** Uline. Brazil and Bolivia.

D. macroura Harms. = *D. sansibarensis*.

D. (Cardiocapsa) **mamillata** Jum. & Perr. Northern Madagascar.

D. (Enantiophylllum) **mangenotiana** Miège. A very large species of Guinea.

D. martinicensis Spreng. = *D. polygonoides*.

D. (Cycladenium) **megalantha** Griseb. Argentine.

D. (Lasiophyton) **melanophyma** Pr. & Burk. Himalaya to Yunnan.

D. (Stenophora) **membranacea** Pierre. Indo-China.

D. (Polyneuron) **minima** Robins. & Seaton. A dwarf of Mexico.

D. (Enantiophyllum) **minutiflora** Engl. Tropical Africa.

D. (Monadelpha) **monadelpha** Pax. Southern Brazil.

D. (Monadelpha) **monandra** Hauman. Argentine. Presumedly an abnormality.

D. multicolor Linden & André = *D. amarantoides*.

D. (Sphaerantha) **multiflora** Mart. South tropical South America.

D. (Polyneuron) **multinervis** Benth. Mexico.

D. (?, uncertain) **mundtii** Baker. South Africa.

D. (Brachyandra) **nako** Perr. A peculiarly slender species of Madagascar.

D. (Stenophora) **nipponica** Makino. Japan and near parts of eastern Asia.

D. (Enantiophyllum) **nummularia** Lamk. The commonest species of its section in eastern Malaysia and Papua.

D. (Enantiophyllum) **odoratissima** Pax. A considerable species of Guinea.

D. (Enantiophyllum) *opposita* Thunb. Widely in subtropical eastern Asia, the Chinese Yam, wild and cultivated. *D. opposita* is the legitimate name for what is widely called *D. batatas*.

D. (Enantiophyllum) **orbiculata** Hook. A considerable species of western Malaysia.

D. (Pachycapsa) **ovinala** Baker. West and central Madagascar.

D. (Opsophyton) **paleata** Burk. Central Africa.

D. (Stenophora) **panthaica** Pr. & Burk. South-west China.

D. (Stenocorea) **paradoxa** Pr. & Burk. Peninsular Siam.

D. (Lasiophyton) **pentaphylla** L. Very widespread in tropical Asia and to the remote islands of the Pacific. There are cultivated races.

D. (?Pedicellatae) **perdicum** Taubert. A dwarf of south-east Brazil.

D. (Centrostemon) **piperifolia** Humb. & Bonpl. Tropical South America.

D. (Paramecocarpa) **piscatorum** Pr. & Burk. A very vigorous species of western Malaysia.

D. (Pedicellatae) **plantaginifolia** R. Knuth. Southern Brazil.

D. (Polyneuron) **platycolpota** Uline. Mexico.

D. (Sarcocapsa) **plumifera** Robins. A small species of Mexico.

D. (Enantiophyllum) **polyclades** Hook. f. A vigorous species of western Malaysia.

D. (Lychnostemon) **polygonoides** Humb. & Bonpl. Widely in the West Indies and northern parts of South America.

D. porteri Pr. & Burk. = *D. kingii*.

D. (Monadelpha) **praetervisa** R. Knuth. Argentine.

D. (Macrocarpaea) **preussii** Pax. A considerable species of Guinea.

D. (Cardiocapsa) **proteiformis** Perr. A very curious species of eastern Madagascar.

D. (Shannicorea) **pseudo-nitens** Pr. & Burk. Siam.

D. (Brachyandra) **pteropoda** Bovin. North and east Madagascar.

D. (Enantiophyllum) **puber** Bl. A rather large species of India and Malaysia.

D. pusilla Hook. = *D. humilis*.

D. (Borderea) **pyrenaica** Bubani. A dwarf of the Central Pyrenees, chiefly on the Spanish side.

D. (Enantiophyllum) **pyrifolia** Kunth. The commonest of its section in western Malaysia.

D. (Lasiophyton) **quartiniana** A. Rich. A very widespread species of rather open lands in tropical Africa.

D. (Stenophora) **quinqueloba** Thunb. Japan and North China.

D. repanda Bl. A youth form of one of the Enantiophylla, almost always *D. pyrifolia*.

D. (Lasiophyton) **retusa** Mast. Southern tropical Africa.

D. (Enantiophyllum) **rotundata** Poir. The white Guinea Yam.

D. (Rhacodophyllum) **rupicola** Kunth. Subtropical southern Africa.

D. (Brachyandra) **sambiranensis** R. Knuth. Madagascar.

D. (Macroura) **sansibarensis** Pax. A very large species of equatorial Africa.

D. sativa Thunb. is a synonym for *D. bulbifera*, much used at one time; but Delpino apparently applied it to *D. alata*.

D. (Asterotricha) **schimperiana** Hochst. From Abyssinia southwards.

D. schliebenii R. Knuth. A variety of *D. quartiniana*.

D. (Lasiophyton) **scortechinii** Pr. & Burk. Indo-China and Malaya.

D. (Asterotricha) **semperflorens** Uline. Equatorial Africa. Its specific name refers to its uncertain season of flowering.

D. (Seriflorae) **seriflora** Jum. & Perr. Northern and western Madagascar.

D. (Enantiophyllum) **sexrimata** Burk. Celebes.

D. (Illigerastrum) **simulans** Pr. & Burk. South-east China.

D. (Brachystigma) **sinuata** Vell. Subtropical South America.

D. (Enantiophyllum) **smilacifolia** De Wild. A large species of Guinea.

D. (Brachyandra) **soso** Jum. & Perr. A species of Madagascar with some of the characters of *D. hexagona*.

D. (Enantiophyllum) **spicata** Roth. Ceylon and southern India.

D. (Dematostemon) **stenophylla** Uline. In savannahs of south-central Brazil.

D. (Testudinaria) **sylvatica** Ecklon. Subtropical South Africa.

Dioscorea synandra Standley, non Uline = *D. gaumeri*.

D. (Polyneuron) **tacambensis** Lunnell. Mexico. A close ally of *D. platycolpota*.

D. (Stenophora) **tenuipes** Franch. & Sav. Japan.

D. (Stenophora) **tokoro** Makino. Japan and the eastern edge of Asia.

D. (Macrogynodium) **trifida** L. West Indies and northern part of S. America.

D. (Trifoliatae) **trifoliata** Griseb. Northern parts of South America.

D. triphylla L. in 1754, but not in 1753 = *D. hispida*. Grisebach's American '*D. triphylla*' was a chimaera of *Clematis dioica* and *D. polygonoides*.

D. (Seriflorae) **tsaratananensis** Perr. Northern and central Madagascar.

D. (Rhacodophyllum) **undatiloba** Baker. South-east tropical Africa.

D. variifolia Kunze = *D. sinuata*.

D. (*Lasiophyton*) *verdickii* De Wild = *D. quartiniana*.

D. (Stenophora) **villosa** L. A rather small species of the eastern United States. The name has been used for *D. glauca* by some writers.

D. (Enantiophyllum) **wattii** Pr. & Burk. A rather large species of North-east India.

Rajania cordata L. West Indies.

R. *cordifolia* Becc. inadvertently for *R. cordata*.

R. sintenisii Uline. Porto-Rico.

Stenomeris dioscoreifolia Planch. North-east Borneo and the Philippine Islands.

S. borneensis Oliv. Sumatra to Borneo.

Tamus communis L. Atlantic Islands, through western Europe and the Mediterranean.

Trichopus zeylanicus Gaertn. Ceylon, south India and north-east Malaya.

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Growth, development, and effect of the environment on the ultra-structure of plant surfaces*

By BARRIE E. JUNIPER

The Botany School, University of Oxford

Communicated by Dr W. G. Templeman, F.L.S.

It has been demonstrated in many species of plants that wax is extruded or migrates on to the surfaces of the leaves and stems, both as a smooth layer and in a structural form which results in a visible 'bloom' (Juniper, 1959). Where a bloom is formed the carbon replica technique reveals under the electron microscope minute projections from the cuticle surface of many different forms (Juniper & Bradley, 1958). The discovery of these wax projections on plant surfaces immediately raises the problem of how such fine structures develop and whether they may be modified by the environment. The size and density of the wax projections found on leaves which are as small as it is possible to handle are practically identical with those on fully grown mature leaves. This seems to indicate that wax formation takes place at a very early stage in leaf development. It also seems to indicate that, because the density of the projections in the mature leaves of most waxy species is only a little less than in the very young leaves, continuous production of wax during leaf expansion must be taking place. Because of the difficulty of handling very small leaves in making carbon replicas, it would have proved very difficult to follow the formation of leaf wax by taking replicas from successively smaller leaf primordia. It was thought possible that the development of leaf wax, since folded leaves have no visible bloom, is stimulated by light, and the following experiment was planned to study the growth of leaf wax under artificial conditions, by totally depriving the developing leaves of light at an early stage.

Peas (*Pisum sativum* var. Alaska) were grown in sand in total darkness at 18° C. for 8 days and were then transferred to a light intensity just below 5000 ft.-candles (approximately full summer daylight). Carbon replicas were immediately taken from the minute leaves which had already developed and successive replicas were taken from corresponding leaves every 24 hr. The development of both the adaxial and abaxial leaf surfaces was followed simultaneously, and the results of this are shown in Pls. **1**–**3**.

Both the appearance (under the electron microscope) and the contact angle of the surface of a pea leaf grown in darkness are very similar to those of dicotyledonous species, which have no apparent surface wax projections (cf. Pls. **1***a*, **6***a* and **7***a*).

Pl. **1***a* shows the adaxial surface of a pea immediately after transfer from darkness to light, and at this point the adaxial surface is very similar to the abaxial, although they become very different from one another later on. The development of the wax on the adaxial surface appears to begin immediately the plants are transferred to light. Twenty-four hours after transfer (see Pl. **1***b*) minute 'crystals' of wax, still disorganized in shape and distribution begin to appear on the adaxial surface. The abaxial leaf surface, away from the light, seems to lag behind in development at this stage and the appearance shown in Pl. **2***d* persists until about the third day. Pl. **1***c* shows the stage of development of the adaxial surface by the second day; the crystals are now clearly distinguishable from the background and are beginning to assume a regular shape. In contrast to the

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observations of Mueller, Carr & Loomis (1954), no pores or pits through which the wax could have been extruded have ever been seen in the pea or in any other species with a waxy bloom. Since the appearance of Pl. **1**b suggests very strongly that prior to the contact with the atmosphere the wax is still in a liquid form, it seems unlikely that any surface replica technique will reveal extrusion pores. Such pores, if present, would be below the level of resolution of the light microscope and could only be resolved by some ingenious form of counter-staining and ultra-thin-sectioning which would distinguish them from the surrounding pectin and cutin layers. Pls. **1**d and **2**a show, at different magnifications, the appearance of the adaxial surface after 3 days. The crystals have completely covered the leaf surface with the exception of the guard cells around the stomata, but they are still angular with more or less straight sides and have only reached about $0{\cdot}6\,\mu$, two-thirds of their ultimate height.

On the fourth day after transfer, changes can be seen for the first time on the abaxial surface. This is shown at different magnifications in Pls. **3**a and b. From this point development on the lower side of the leaf proceeds very rapidly. Projections completely cover the lower surface of the leaf by the end of the fourth day and by the fifth day (compare Pl. **3**c with **2**b and **2**c) the abaxial surface has drawn level in development with the adaxial, although, as is clear from the micrographs, the final result is entirely different at the submicroscopic level. From the seventh day after transfer (see Pl. **3**d) no further changes are observed in the fine structure of the leaf; the crystals on the adaxial surface no longer have the angular appearance of those in Pl. **1**c; those on the abaxial surface have likewise lost the peg-like appearance of Pl. **3**b and have developed into an interlocking mesh.

It is, of course, only conjecture that the progress of the fine structure of the leaf surface from the primordial to the mature leaf follows this pattern. But this is of some importance for undersown crops or weeds growing under crops which are later harvested may be faced with such a situation (a rapid transfer from low to high light conditions) and it seems likely that the pattern of development illustrated above resembles that occurring under natural conditions.

One of the most remarkable features of the development of these surface waxes is that growth is determinate. Therefore, analogies with such phenomena as 'myelin tubes' (see Frey-Wyssling, 1948), in which growth is both uncoordinated and continuous, cannot be drawn. All the species with a wax bloom that I have examined appear to have projections that grow only to a critical length or size. The branched wax tubes of *Chrysanthemum segetum* (Pl. **4**a) extend to a maximum of about $2\,\mu$ and then cease growth. The tubes of this species appear to be smooth even under the highest magnification, but several of the surfaces, particularly those shown in Pl. **4**b, c and d, would seem to have projections showing a definite repeating pattern of growth. This pattern is particularly noticeable in the cabbage *Brassica oleracea* var. *capitata* (Pl. **4**b) and the three tubes just below and left of centre in this micrograph have a quite striking segmented appearance. A small group of tubes at a much higher magnification is shown in Pl. **4**c. The suggested interpretation of this surface is that small ($0{\cdot}25$–$0{\cdot}5\,\mu$) and more or less annular areas in the cuticle of the young leaf begin to secrete wax on to the surface. As the leaf ages and enlarges these secretory rings become larger, more areas of secretion are formed and two or more of these rings may fuse together to give fasciated bundles of projections. The upper left-hand edge of Pl. **4**b is probably an example of the result of such a fusion. The expansion of the areas of secretion would also explain why many of the tubes appear to taper from the base (see Pl. **4**c). The walls of these tubes are extremely thin (this can be seen clearly in Pl. **4**c) and the tubes themselves very delicate, so that, even in plants grown in the constant temperature room, the majority of the tubes will have broken off and will be lying on their sides.

Evidence from wiping the surface off cabbage leaves at regular intervals indicates that wax production continues until a very late stage in leaf expansion, so that the surface of an old cabbage leaf is made up of a tangled mass of broken wax tubes with wax production still continuing at the base of the tubes. It is tempting to suggest that the rings that we see on these wax tubes (Pl. **4***c*) represent some form of phasic growth, as if the wax was not secreted in an even flow but with a more or less regular rhythm. What the relationship is between these 'growth rings' and the age of the wax tube itself is not yet clear. Nor is it clear why the projections of only a very few species have this repeated pattern within each individual projection. It is quite clear, however, even from casual observation, that extension in depth of the wax layer on brassicas does take place; the grey/white surface bloom of the young leaf is replaced, if aerial weathering is not too severe, by the thick blue/green bloom of the old leaf. Growth of the projections does not continue indefinitely but at what point in leaf expansion it ceases, if there is a definite point, has not yet been determined. A restriction in growth can also be seen in those species which secrete wax in the form of tufts. Pls. **5***a* and *b* show good examples, and it appears that whatever the age of the leaf and whatever the environmental conditions these tufts grow to a certain diameter but never fuse to give a uniform layer.

It seems that most plants of the temperate zone with waxy leaves, whether they are of the individual crystal type such as the pea (*Pisum sativum*) or a network of tubes, such as *Chrysanthemum segetum* (Pl. **4***a*), or a carpet of isolated tufts such as *Papaver somniferum* (Pl. **5***a*) or *Kleinia articulata* (Pl. **5***b*) given a comparable environment seem to reach a more or less uniform depth and density of projections and persist. However, there is some evidence that the fine structures on contiguous epidermal cells, or over the surface of a single cell may at any one time be at different levels of development. This is demonstrated in Pl. **5***c* which is of the adaxial leaf surface of *Lupinus albus*. The outlines of the epidermal cells are marked by widely spaced and relatively large wax projections. The centre of each epidermal cell appears to have developed wax projections which are finer, more angular and more densely compressed than those on the margins of the cells. The previous evidence presented suggests that these criteria of small size and angularity indicate an immature surface at an early stage in its development. But, since the conclusion that the centre of an epidermal cell is less mature than the margins is unlikely, another explanation must be sought.

Although, as already mentioned, the fine structure of a leaf's surface will persist when mature, its final form and density may depend on its previous environmental history.

Lee & Priestley (1924) noticed that in some plants the thickness of the cuticle increased as the quantity of available moisture fell and the light intensity rose. More recently Dorschner & Buchholtz (1956), using artificial shade, indicated that a reduction in the available sunlight influenced the morphological development of lucerne (*Medicago sativa*) growing amongst oats so that the wetting capacity of applied chemical sprays was increased. Therefore the following experiment was planned to study the effect of a range of light intensities on the fine structure of the cuticle of peas. All the plants in a single experiment were grown in the same growth chamber and the different light intensities were achieved by interposing one or more layers of butter muslin between the light source and the plant. The light intensities were measured at the level of the second leaf, the leaf that was used for the experiment, and not at ground-level.

Peas grown in the dark have leaves which are very small, yellow and shiny and their surfaces are very difficult to replicate. Their appearance (Pl. **6***a*) under the electron microscope and their contact angle (68°) are reminiscent of dicotyledonous plants which have no apparent surface wax such as the beet (*Beta vulgaris*) (Pl. **7***a*). Pl. **6***b* shows the adaxial surface of a pea grown at 900 ft.-candles. The surface is completely covered with fine structure and is remarkably uniform. The wax projections are regular, rarely more than $\frac{1}{2}\mu$ high, have more or less straight sides, and are closely bunched together. The individual platelets of the projections are thin and are still mostly transparent to the electron beam. The over-all picture changes only a little at 1500 ft.-candles. The individual projections themselves are nearly twice as large in all dimensions and are opaque to the electron beam but they still have more or less straight sides. At 5000 ft.-candles (Pl. **6***d*) development of the fine structure seems to have reached its peak. The difference is even apparent to the eye in an increased whiteness of the surface as compared to the pea surface corresponding to Pl. **6***c*.

The individual crystals are only a little thicker than in Pl. **6***c*, but their margins have developed to such an extent that the background is almost entirely obscured. However, the contact angle of peas grown in light intensities over the range 5000–900 ft.-candles remains close to 140°. This must be due to the whole surface being covered with projections, even at 900 ft.-candles. The lowering of the light intensity incident on pea leaves within the range that one could expect to encounter in the field seems therefore unlikely to make much difference to the actual wettability of the surfaces. However, the differences in the density, the height and the interlocking of the individual projections at different light intensities might well be significant where aerial weathering was severe. The less well-developed surfaces would be more severely affected by mechanical damage, and peas are known to be susceptible to this type of damage. In this context the effect of a high wind speed on the growth of the fine structure of a leaf's surface is interesting. Pl. **7***b* shows an adaxial leaf surface of a pea from a plant grown in a wind tunnel with a wind of 25 m.p.h. If this is compared with Pl. **6***d* of a plant of comparable age grown in still air, differences are immediately apparent. Although the contact angles of the two surfaces are similar it would appear that a high wind speed results in shorter, thicker and more dense projections from the surface; all these features would tend to increase resistance to abrasive damage. One of the effects of mechanical damage would be to increase the wettability of the surfaces and this may have contributed to the enhanced retention noticed by Dorschner & Buchholtz.

The appearance of these micrographs, particularly when seen in transverse sections (Pl. **7***c*) suggests strongly that mechanical damage might be an important factor in the wettability of plant surfaces. It is a common observation amongst agronomists that the amount of mechanical damage inflicted on an individual plant's surface affects the susceptibility of those plants to herbicides subsequently applied (see Dewey, Gregory & Pfeiffer, 1956). The effect varies from crop to crop, slowly grown plants in general tending to be more resistant than those grown rapidly. Only some species of plants, moreover, seem to be susceptible to mechanical damage to their wax covering.

It is very difficult to relate general observations of this kind to differences observable in the laboratory. However differences in growth rate do result in differences in the ultra-structure of the surfaces of some plants, and they could be connected with their response to mechanical damage. For example, Pl. **8***a* shows the stem surface of a very rapidly grown cabbage. The individual wax tubes are widely spaced and, as such, lacking in mutual support, would be very susceptible to mechanical damage. The leaf surface of a more slowly grown cabbage is shown in Pl. **4***b*. The leaves of cabbages, in which root growth is severely restricted, are limited in size but develop a thick blue bloom on the cuticle which is visible under the electron microscope as a tangled mass of tubes, some crushed and flattened and others still intact and erect. There is some evidence, as already mentioned, that separate sites of extrusion may join up with one another (Pl. **4***b*) and new isolated sites may develop in between with the result that, in old leaves, the background is almost completely obscured. Some leaves, therefore, which grow slowly have a thicker layer of wax projections developed on all their surfaces and this may contribute both to their resistance to mechanical damage and possibly also to the increased resistance to herbicides observed.

However, different species of plants, as well as the same plants grown under different conditions, seem to react differently to mechanical damage. Also, if damaged, some seem to possess powers of recovery, during at least the early stages of their development. The differences between species are obvious even to casual examination; the hyacinth

(*Hyacinthus orientalis*) and the daffodil (*Narcissus pseudonarcissus*) lose their water repellent bloom very rapidly, and, only a very short time after leaf emergence, their surfaces are completely wettable. The cabbage is rather better protected and only old mature leaves which have been subjected to considerable abrasion are usually wettable. A very few species, such as *Oxalis corniculata*, retain the ability to repel water droplets indefinitely. The degree of resistance offered by a plant to mechanical damage could depend on the composition of the wax of which the outermost layers of its cuticle were formed or the form taken by the wax projections.

The hardness of a wax will depend on a number of factors, including the conditions under which it is grown and its rate of growth. However, so very little is known about the comparative chemistry of plant waxes that it is very difficult to use such data as are available. On the other hand, an examination of the fine structure has proved very interesting if not conclusive. If we take the extremes of the series, as far as susceptibility to damage is concerned (*Hyacinthus orientalis* and *Oxalis corniculata*), differences in the projections are immediately apparent. The fine structure of *Hyacinthus orientalis* (Pl. **8***b*) is an irregular pattern of very fine sheets of wax, giving the impression that they have just peeled away from the surface like strips of the bark from a tree. The individual sheets seem to have no preferred orientation and rarely touch one another. The appearance of the *Oxalis* surface (Pl. **4***d*) is completely different. The individual projections are star-shaped and are therefore less likely to be pushed over; they are so close together as to make it impossible to see the background and the individual segments of the projections interdigitate to form a mutually supporting mesh. Although the initial contact angles of these two surfaces are the same (above 140°) the leaf surface of the *Hyacinthus* is readily damaged even by watering from above in the greenhouse and, out of doors, the surface is usually wettable within a few days of the unfolding of the leaves. The leaves of the *Oxalis*, even in exposed situations, remain unwettable indefinitely and unlike most species, the yellow and senescent leaves still have a contact angle above 140°. Similar to the *Oxalis* in its resistance to mechanical damage is *Juncus inflexus* (Pl. **8***d*). In this species the sharply ridged epidermis is covered by a *smooth* cuticle. The heavily thickened sclerenchyma below the ridges, the hard cuticle and the vertical positioning of the leaves combine to make a surface almost impervious to damage. Apart from this special case, in which the gross morphology of the leaf is the significant factor, the appearance of the micrographs of the surfaces seems to be a good guide to the qualities of those surfaces. The pea, for example (Pl. **6***d*) is similar to *Oxalis* in its fine structure, but the projections are less dense and do not interlock to quite the same extent. The pea leaf is somewhat more susceptible to mechanical damage than *Oxalis*, but is among the most resistant of cultivated plants, particularly when grown slowly. Similar in properties to the pea leaf is the surface of *Chrysanthemum segetum* (Pl. **4***a*); the entangled mass of wax tubes is not readily crushed (Pl. **8***c*) nor easily washed away. Similarly, in *Brassica oleracea* even if the tubes are broken and pushed over they retain enough of their structure to preserve the micro-roughness necessary for a high contact angle. Pl. **9***b* shows a cabbage which has suffered severe field weathering and on which considerable quantities of soot have landed. Although almost all the fine structure of the original surface has disappeared, neither the tubes themselves, nor the bases of those tubes are sufficiently crushed to depress the angle below 140°; all the fine structure, it seems, must be eroded away before the contact angle is reduced. Many species, such as *Galanthus nivalis* (Pl. **9***a*) have wax projections on their surfaces which are too widely spaced and too delicate to avoid being flattened or brushed away.

Only a few species have been observed to recover from mechanical damage and re-establish a high contact angle. If the surface of a young leaf of *Chrysanthemum segetum* s brushed vigorously the contact angle falls to just below 100°. But within 7 days, if the eaf is not too badly damaged in the initial treatment, the surface regenerates and the contact angle rises above 140° again. This only occurs if the leaf is damaged before leaf expansion has ceased. *Brassica oleracea* recovers rapidly at first but the ability to recover ceases before leaf expansion ceases. But in the majority of species with waxy surfaces recovery does not take place at all; it has never been seen, for example, in the Leguminosae.

The present research has revealed, in greater detail, the fine structure of a part of the cuticle. It has not elucidated any further the processes by which the cuticle is formed, and, in fact, this evidence means that we must modify the theories of development of the cuticle put forward by Priestley (1943) and later by Scott, Hamner, Baker & Bowler (1958). We must add a complete stage to the process of the development of the cuticle; a stage which is distinct from and has apparently no connexion with the formation of the pectin and the cutin layers. There is no evidence, moreover, to suggest, as has been put forward, that the wax ultrastructure of the plant surface is connected with plasmodesmata. My observations agree with those of Schieferstein & Loomis (1956) that there is as yet no evidence for the existence of definite pores through which the wax is extruded or migrates. It seems unlikely that the process of wax extrusion is even indirectly connected with plasmodesmata. The density of plasmodesmatal strands recorded is not above $36/100\mu^2$ (Esau, 1953). This is much lower than the density of distinct wax projections seen on any of the surfaces which may be up to $400/100\mu^2$. Plasmodesmata have, moreover, rarely been found in epidermal cells. It seems then that the processes by which the layers of the cuticle are formed will have to await both advances in cuticular chemistry and in techniques for the sectioning of plant material for the electron microscope.

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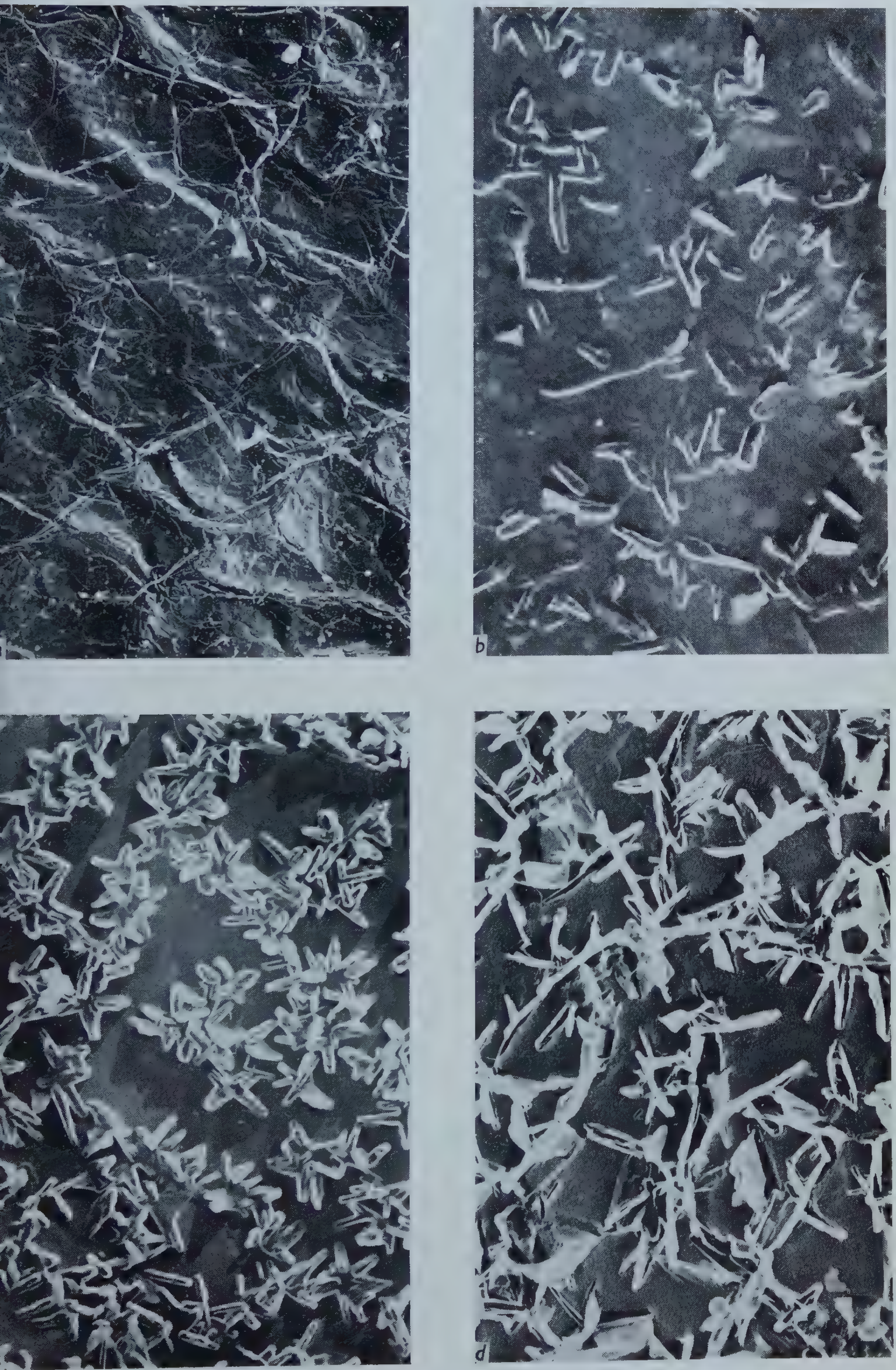
EXPLANATION OF PLATES 1–9

PLATE 1

a. Adaxial leaf surface of *Pisum sativum* grown in darkness to second leaf stage. × 1100.
b. The same 24 hr. after transfer to light. × 12,400.
c. The same 48 hr. after transfer to light. × 12,400.
d. The same 72 hr. after transfer to light. × 12,400.

Plate 1



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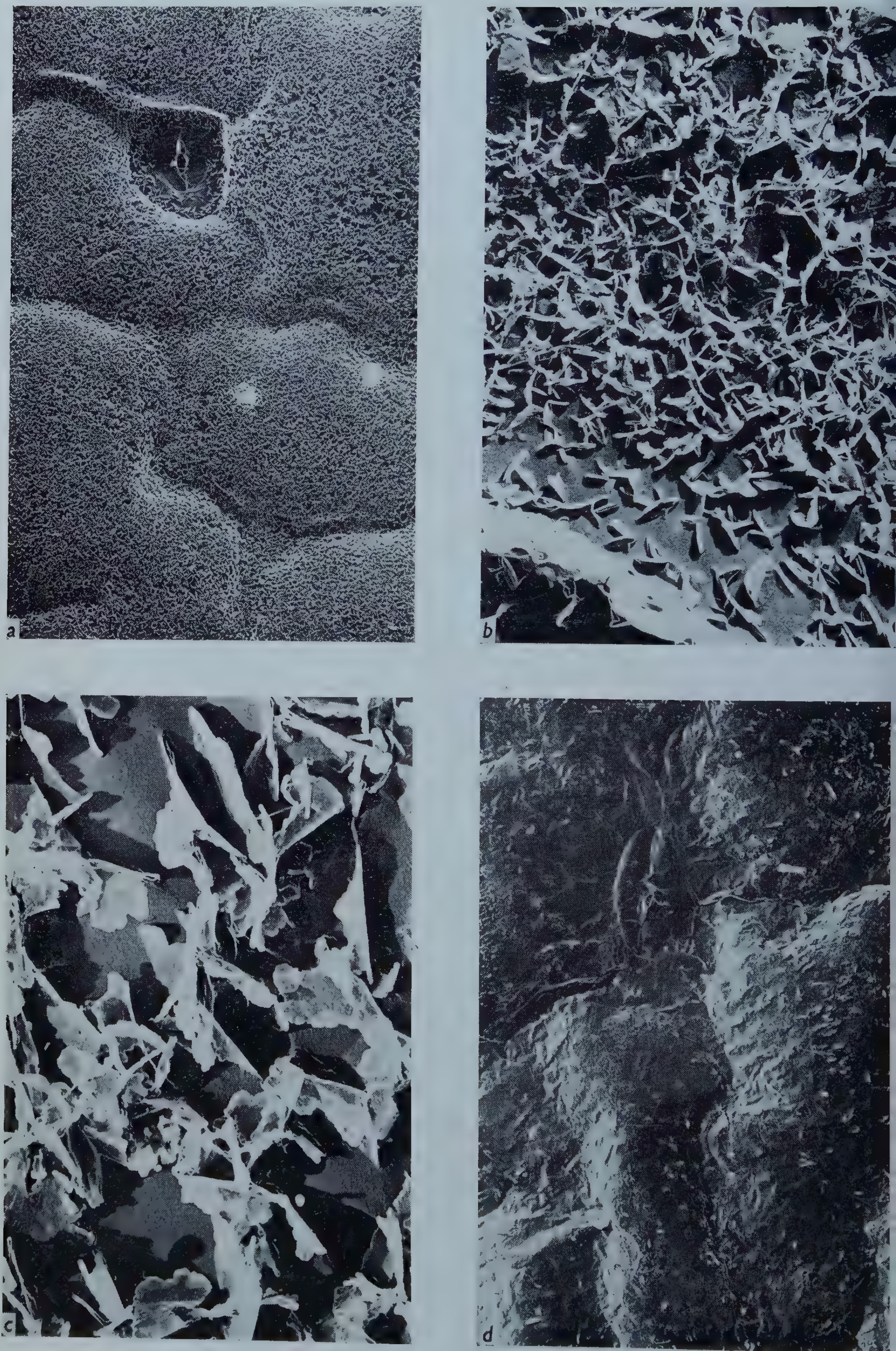

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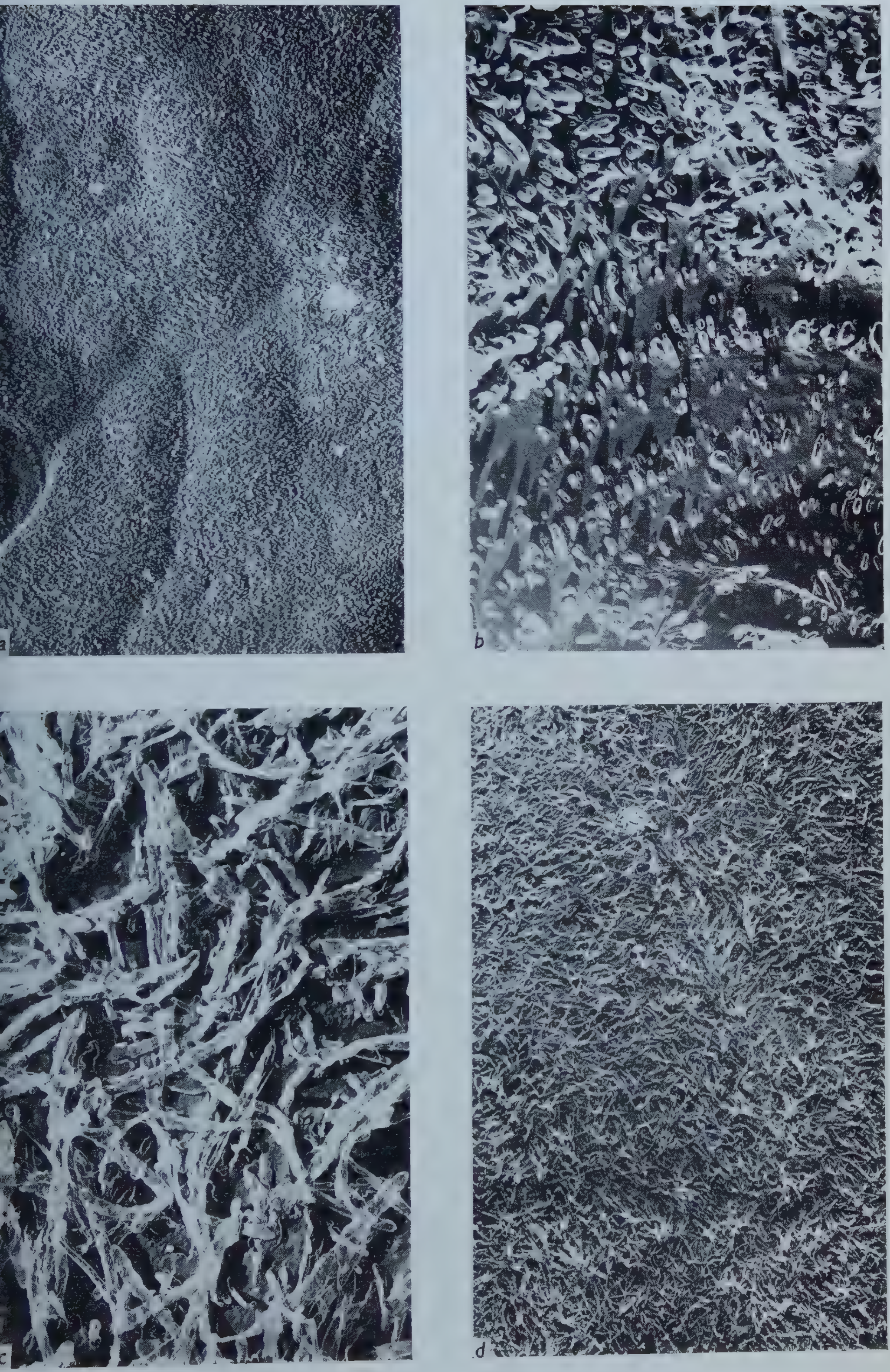
Plate 3



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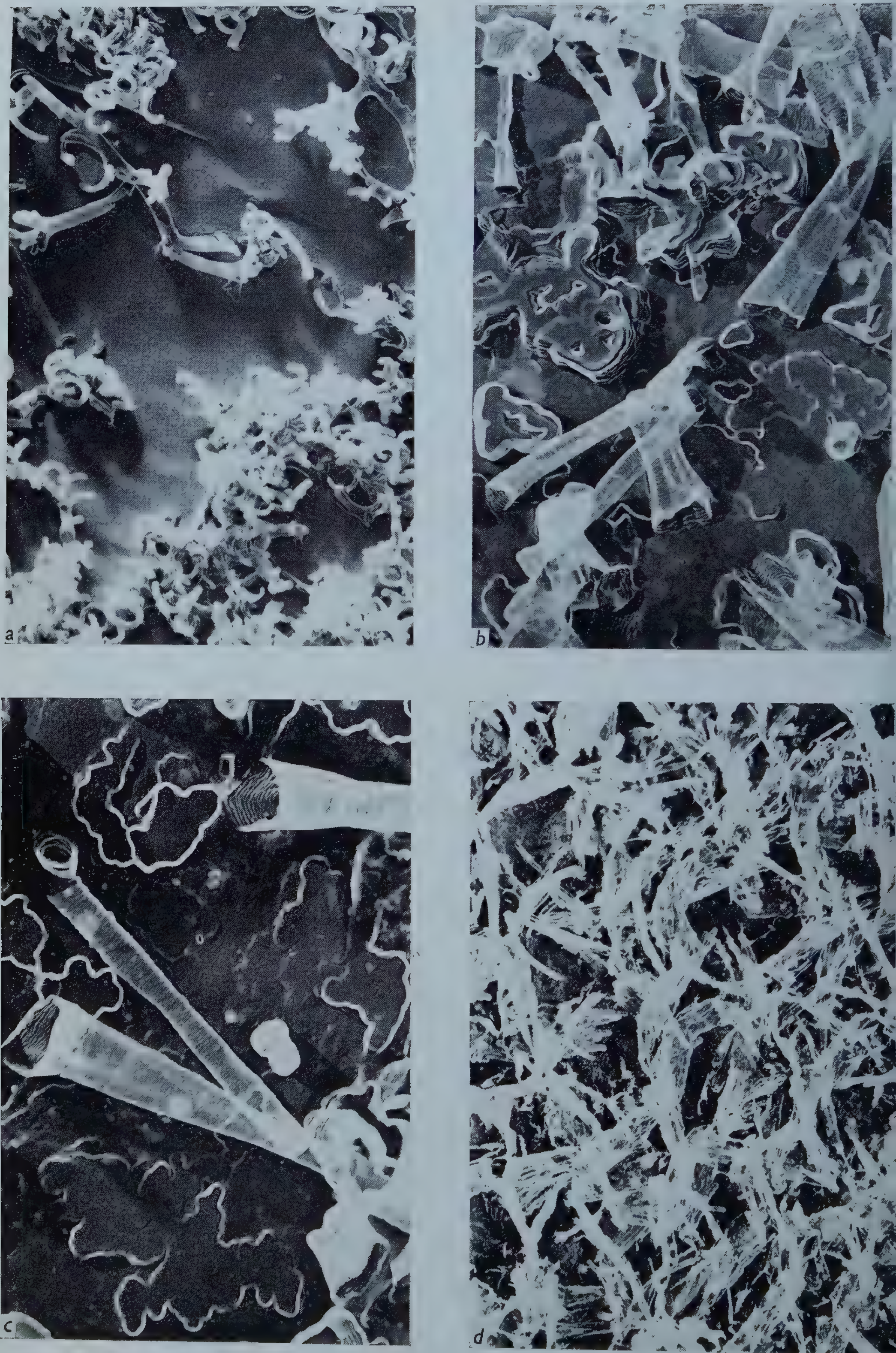
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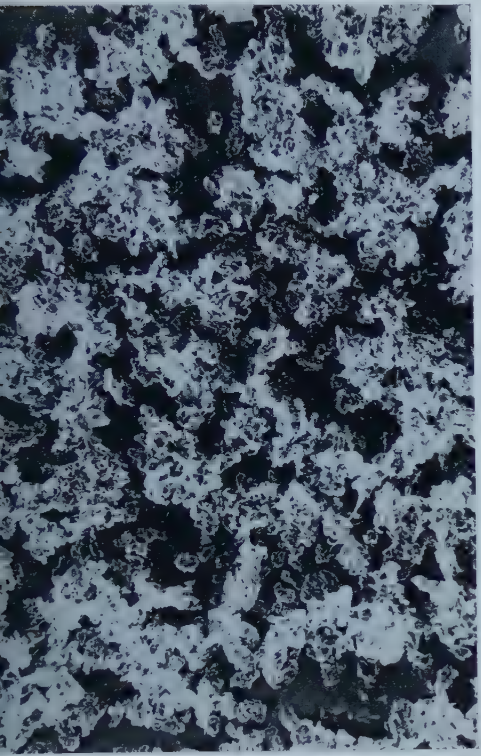

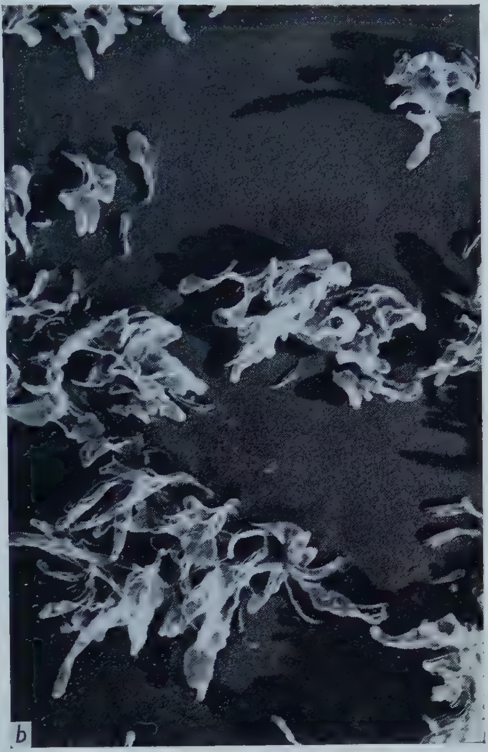

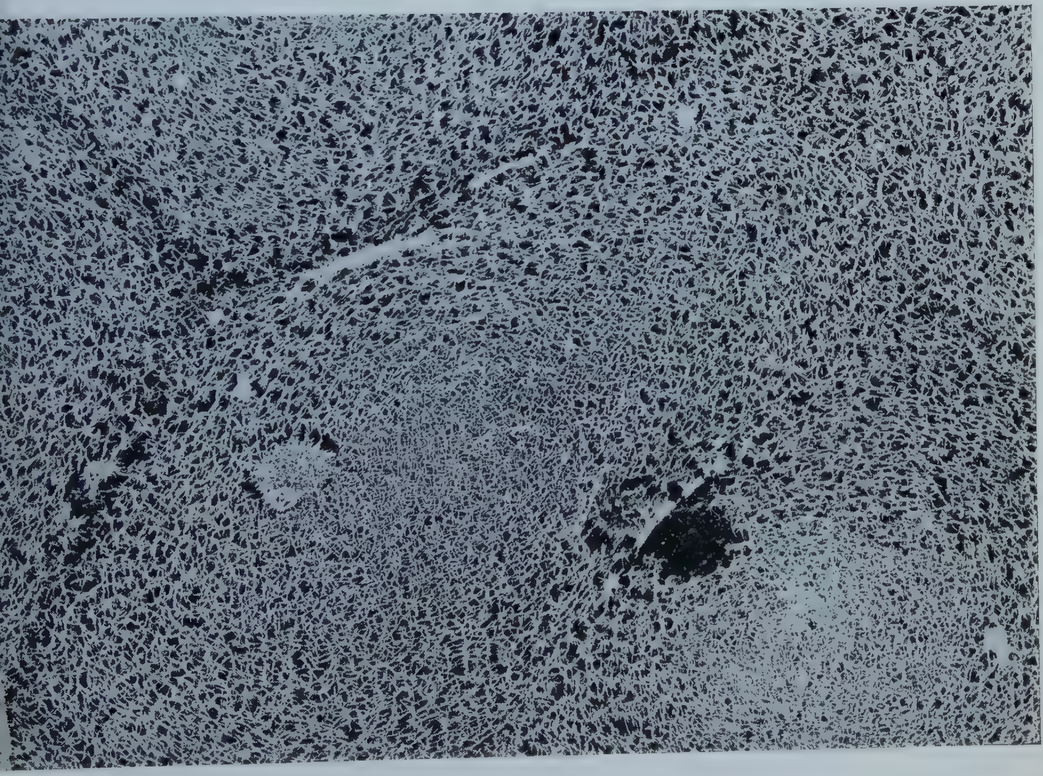

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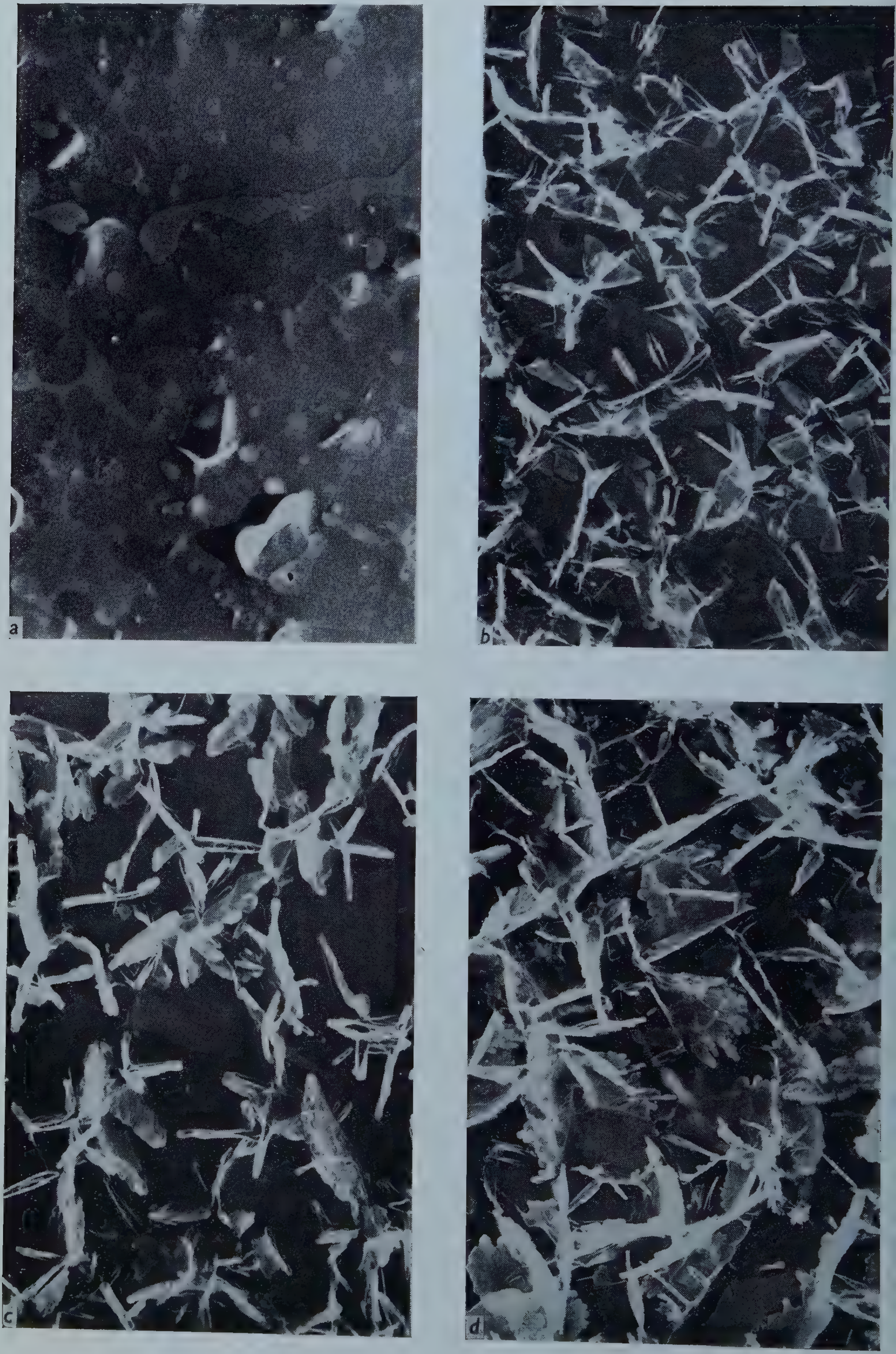
Plate 6



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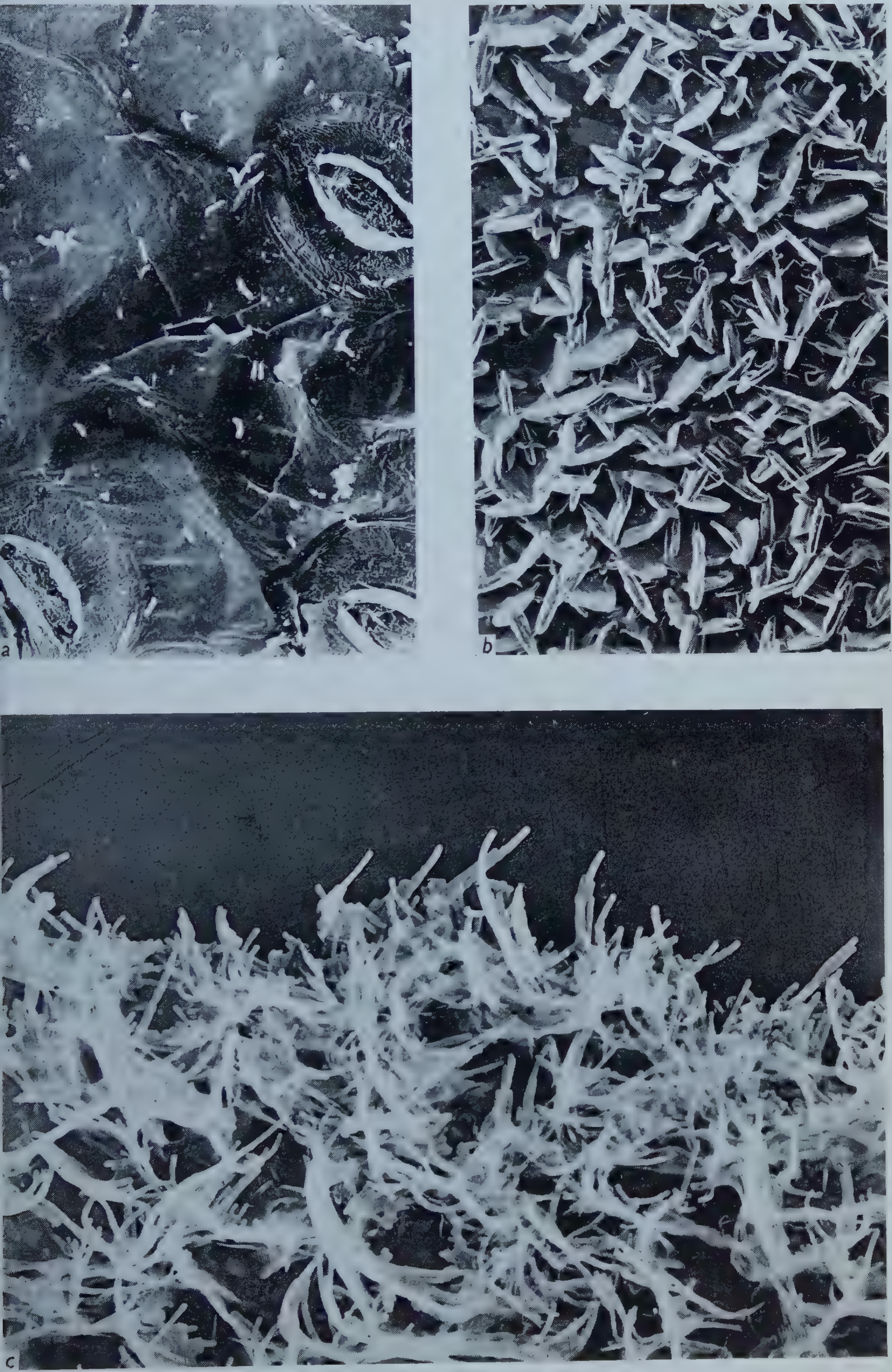

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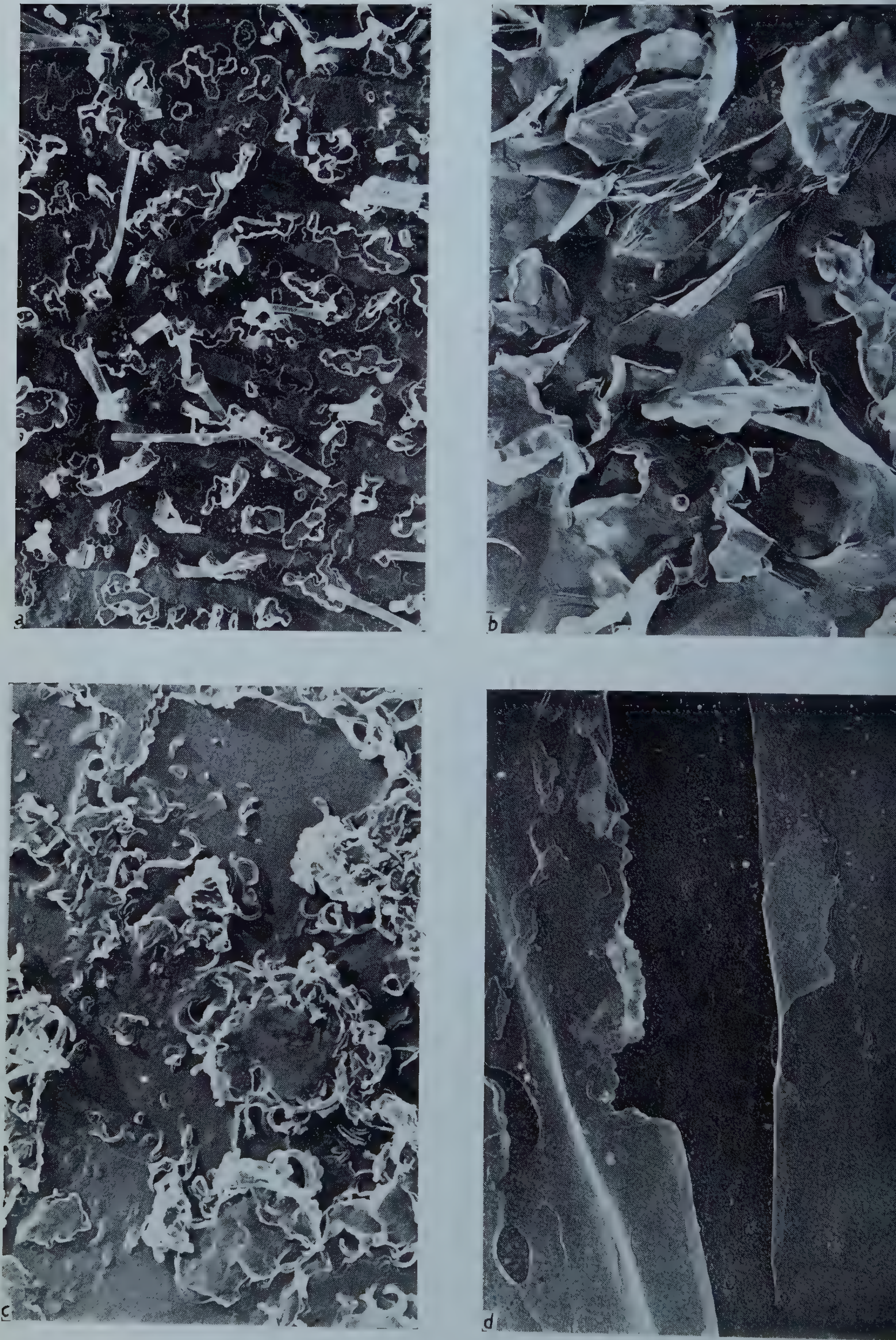

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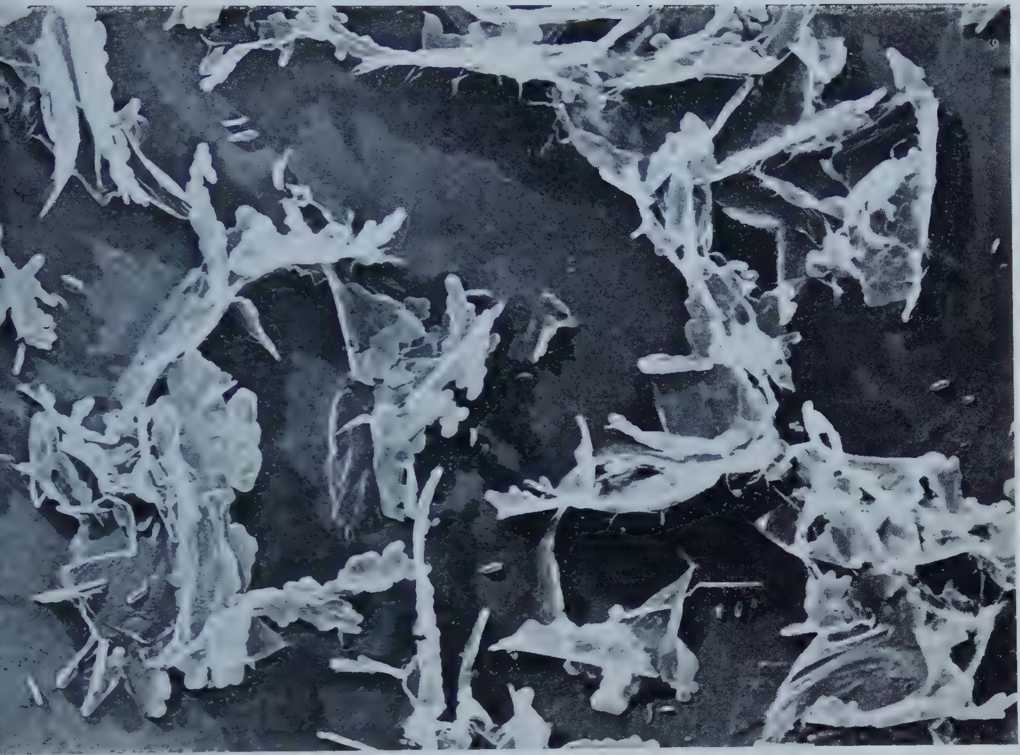

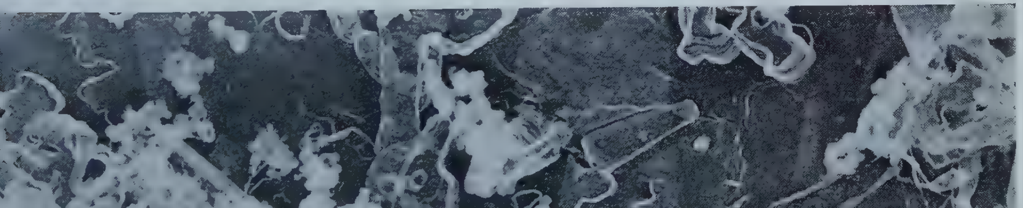

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PLATE 2

a. Adaxial leaf surface of *Pisum sativum* 72 hr. after transfer to light. × 1100.
b. The same 5 days after transfer to light. × 8800.
c. The same 7 days after transfer to light. × 12,400.
d. Abaxial leaf surface 3 days after transfer to light. × 1100.

PLATE 3

a. Abaxial leaf surface of *Pisum sativum* 4 days after transfer to light. × 1100.
b. The same 4 days after transfer to light. × 8800.
c. The same 5 days after transfer to light. × 8800.
d. The same 5 days after transfer to light. × 1100.

PLATE 4

a. Adaxial leaf surface of *Chrysanthemum segetum*. × 12,400.
b. Adaxial leaf surface of *Brassica oleracea* var. *capitata*. × 12,400.
c. Adaxial leaf surface of *Brassica oleracea* var. *capitata*. × 19,200.
d. Adaxial leaf surface of *Oxalis corniculata*. × 12,400.

PLATE 5

a. Adaxial leaf surface of *Papaver somniferum*. × 8800.
b. Adaxial leaf surface of *Kleinia articulata*. × 12,400.
c. Adaxial leaf surface of *Lupinus albus*. × 1100.

PLATE 6

a. Adaxial leaf surface of *Pisum sativum* grown in darkness. × 12,400.
b. The same grown at 900 ft.-candles. × 12,400.
c. The same grown at 1500 ft.-candles. × 12,400.
d. The same grown at 5000 ft.-candles. × 12,400.

PLATE 7

a. Adaxial leaf surface of *Beta vulgaris*. × 1100.
b. Adaxial leaf surface of *Pisum sativum* grown in wind-tunnel at 25 m.p.h. wind-speed. × 12,400.
c. Adaxial leaf surface of *Lupinus albus*. The carbon film has been broken on the grid, has bent over, and has been photographed at right angles to the normal plane of viewing. × 18,000.

PLATE 8

a. Stem surface of *Brassica oleracea* var. *capitata*. × 6600.
b. Adaxial leaf surface of *Hyacinthus orientalis*. × 12,400.
c. Adaxial leaf surface of *Chrysanthemum segetum* damaged by brushing. × 12,400.
d. Leaf surface of *Juncus inflexus*. × 12,400.

PLATE 9

a. Adaxial leaf surface of *Galanthus nivalis*. × 18,000.
b. Adaxial leaf surface of *Brassica oleracea* var. *capitata* grown in the open and heavily contaminated with soot. × 18,000

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On *Pityostrobus leckenbyi* (Carruthers) Seward and *Pityostrobus oblongus* (Lindley & Hutton) Seward, fossil abietaceous cones from the Cretaceous

By G. T. CREBER, F.L.S.
University College School, Hampstead

INTRODUCTION

The present investigation commenced with the detailed anatomical study of two cones, from the Albian-Crenomanian of the Argonne, loaned by the Director of the Ecole Nationale Supérieure de Géologie Appliquée, Nancy. These cones had originally been described by Fliche (1896) in broad outline and identified as *Cedrus oblonga*, first recorded by Lindley & Hutton (1835) from the Upper Greensand of Dorset. Fliche realized of course that his cones also bore an immediate resemblance to *Pinites leckenbyi* (Carruthers, 1866) from the Lower Greensand of the Isle of Wight, but he did not use this name because he considered *Cedrus oblonga* and *Pinites leckenbyi* to be identical and the former name had clear priority. His decision as to the similarity of the two species was based on a comparison of such of the internal structure as was published at that time, comparison of the external being ruled out on account of the considerable abrasion that *Cedrus oblonga* had undergone. Fliche felt, however, that this abraded surface was quite consonant with the kind of surface that would appear if *Pinites leckenbyi* had received similar treatment.

Stopes (1915) was quite opposed to this view; she considered that *Cedrus oblonga* had considerable affinities to the modern genus *Pinus* and hence differed markedly from *P. leckenbyi* which appeared to be truly allied to *Cedrus*. There the matter has rested and it has been tacitly assumed that *C. oblonga* was in fact an abraded pine-like cone, whereas *P. leckenbyi* and Fliche's cones were so obviously like those of the modern genus *Cedrus* that no further discussion appeared necessary.

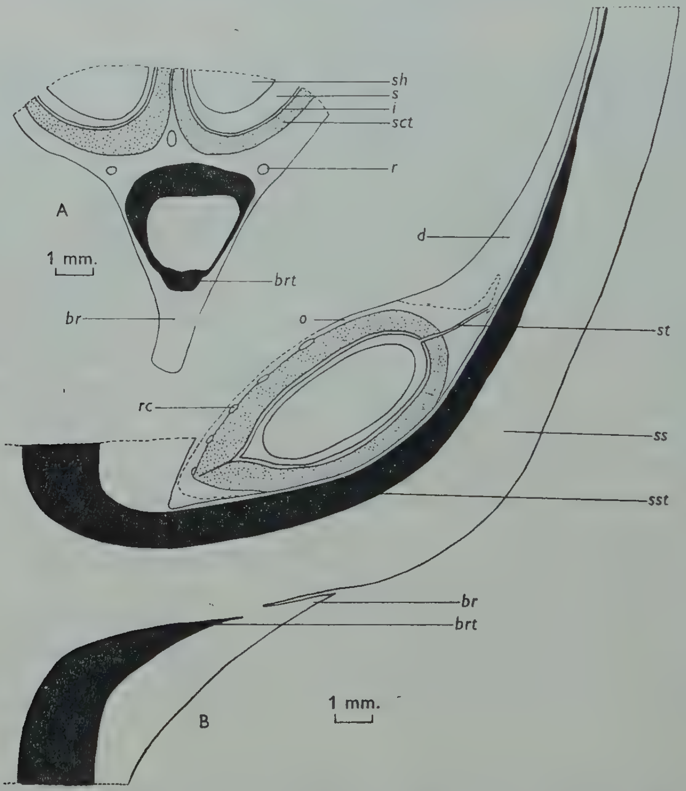
To assess the true relationship of these forms, the anatomy of *Pinites leckenbyi* and *Cedrus oblonga* has been worked out in detail and an appraisal made of the evidence obtained. Through the good offices of the curators of the Geological Museums of the Universities of Oxford and Cambridge it has been possible to investigate the type specimens themselves.

So far in this introduction the original generic names for the specimens have been used. In 1915 Stopes resuscitated Feistmantel's (1874) form-genus *Pinostrobus* for fossil cones resembling those of the modern genus *Pinus* and erected *Cedrostrobus* for those resembling *Cedrus*. Accordingly, *C. oblonga* was placed in *Pinostrobus* on account of its supposed pine-like qualities and *P. leckenbyi* was placed in *Cedrostrobus*. Seward (1919), however, pointed out the dangers of closely allying fossil species with modern types, a view recently reinforced by the work of Alvin (1953, 1957). The latter found that certain fossil cones possessed a mixture of the characters of the cones of modern genera and therefore to place a specimen in a modern genus may at once lead to obvious undesirable anomalies. The modern practice follows Seward in placing all fossil Abietaceous cones in Nathorst's (1897) form-genus *Pityostrobus*. Therefore *Cedrus oblonga* and *Pinites leckenbyi* are both placed in *Pityostrobus*, the former being referred to as *P. oblongus* and the latter as *P. leckenbyi*.

DESCRIPTION OF *PITYOSTROBUS LECKENBYI*

This description is almost entirely based on the type specimen now in the care of the Sedgwick Museum, Cambridge; certain information, not obtainable from the type, was obtained from the Nancy cones which proved to be identical with the type in every respect save size.

The type specimen is a large ovate cone 9·5 cm. long and 5·0 cm. wide at the broadest dimension. The two cones from France are smaller and rather more ellipsoidal in form, one being 9·0 by 4·2 cm. and the other 6·8 by 4·0 cm. They are all calcareous petrifactions and hence particularly suited to the preparation of cellulose peels, which were mounted entire.



Text-fig. 1. *Pityostrobus leckenbyi*. A, vertical section (tangential to the cone) through the fused bases of a seed-scale complex and bract-scale. *br*, bract-scale; *brt*, bract trace; *i*, inner layer of integument; *r*, resin canal; *s*, space caused by shrinkage of the endosperm; *sct*, sclerotesta; *sh*, shrunken endosperm. B, Longitudinal section through the proximal portion of a seed-scale complex and its bract-scale; *d*, decayed chalazal tissue; *o*, outer layer of integument; *rc*, resin cavities; *ss*, seed-scale complex; *sst*, seed-scale complex trace; *st*, seed trace; other labels as for A. (Camera lucida drawings from cellulose peels off the type specimen.)

For the purposes of the original description by Carruthers (1869) the type specimen was cut into two equal halves along the median vertical plane. The external surface of one half and the internal surface of the other were figured in Carruthers's original paper, and these figures are also to be found in Seward (1917). They show the characteristic external form that has led to the association with the genus *Cedrus*. This appearance is due to the fact that the spirally arranged scales are closely imbricated so that only relatively small areas of the abaxial surfaces of their thin broad tips are visible. Furthermore, these tips bear minute vertical striations as do the exposed parts of the scales of *Cedrus*.

The massive axis is by no means constant in diameter along the length of the cone; it is 1·5 cm. wide at the base and tapers to 0·3 cm. at the apex, at the mid-point the diameter is 1·0 cm. The pith, of a similar form, is 0·6 cm. at the base, 0·35 cm. at the mid-point and 0·15 cm. at the apex. The seed-scale complexes consist of ovuliferous scales arising in the axils of the bract-scales to which they are partly fused; the complete bract-scale is 0·6 cm. long of which about 0·2 cm. is free from the seed-scale complex (Text-fig. 1B). The majority of the scales are set at right angles to the axis, although a few at the base are set obtusely and a few at the apex acutely. The rhomboidal zone of attachment to the axis of the fused bract and seed-scale complex is 0·7 cm. wide by 0·7 cm. high. The seed-scale complex is almost horizontal for about 1 cm. and on this part lie the two seeds; the ascending portion being about 2·3 cm. long. The seed-scale complex is 0·3 cm. thick at the point where it diverges from the bract-scale; in the chalazal region the thickness of the seed-scale becomes reduced to 0·2 cm. (Text-fig. 1B), whilst at 1·3 cm. from the actual apex the thickness increases sharply to 0·3 cm. again. The area of the apex exposed on the surface of the cone is 2·8 cm. wide by 0·4 cm. deep. Measurement of the changes in the breadth of the seed-scale in its various regions was not carried out on the type specimen, but similar information was obtained from one of the Nancy specimens (Text-fig. 2). This, however, is a smaller cone and therefore a factor of × 1·25 would have to be applied in order to bring them into line with the dimensions of the type. Two winged seeds are set in each seed-scale, the wing portion of each is poorly preserved, as is the chalazal region, but the ellipsoidal sclerotesta, 0·9 cm. long by 0·4 cm. in diameter, is well preserved (Text-fig. 1B).

Anatomy of the axis. The pith is composed of short cylindrical cells almost circular in cross-section; they are relatively homogeneous, although some appear to have somewhat denser contents. The vascular cylinder is 1·2 cm. in diameter at the base and tapers to 0·7 cm.; at the mid-point it is perforated by gaps associated with the departure of scale traces. The xylem, largely secondary, is 0·3 cm. thick at the base of the cone and 0·2 cm. at the mid-point. It is composed of tracheids with small bordered pits; there are numerous uniseriate rays, but no resin canals. The phloem is not well preserved and the region is largely occupied by secondary iron pyrites. Prominent in the cortex is a system of twenty-one resin canals.

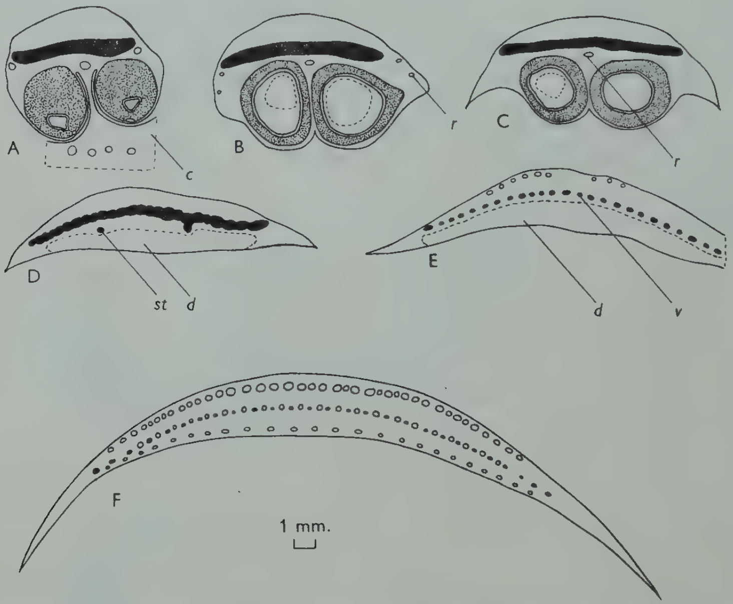
The vascular supply to the seed-scale complex and bract-scale leaves the axial vascular system as a combined cylindrical trace of elliptical cross-section (Text-fig. 3B; Pl. **1**, fig. 4). An oval gap appears in the axial xylem about 0·3 cm. high and 0·1 cm. wide. As the trace enters the cortex it is 0·33 cm. high and 0·25 cm. wide.

Anatomy of the seed-scale and bract-scale. On entry into the fused seed- and bract-scales the cylindrical trace becomes wider and thinner at the sides (Text-fig. 3F; Pl. **1**, fig. 6) so that the individual forms of the seed- and bract-scale trace gradually become more evident. Finally the sides thin out altogether and the seed-scale trace, now a flat band, is entirely separated from the rounded bract trace (Text-fig. 3H). The system of cortical resin canals gives rise to two lateral and a single adaxial resin canals in the seed-scale (Text-figs. 1A; 2A). The two resin canals of the bract-scale appear to arise independently of the axial system.

A section through the seed-scale shows that all the tissue abaxial to the flat band of xylem is sclerenchymatous, as also is the tissue of the extreme lateral portions where the cells are strikingly large and thick-walled. These lateral portions retain their identity for the greater part of the length of the seed-scale, although in the ascending part the cells gradually come to resemble those of the abaxial sclerenchyma; the resin canals are derived from the original lateral canals (Text-fig. 2B). The apical free part of the bract-scale is very thin and is composed of large thin-walled sinuous cells in which are set the two prominent resin canals. In the ascending part of the seed-scale the continuous band of xylem gradually subdivides into a number of small rounded vascular bundles (Text-fig. 2E); in the chalazal region of the seeds two seed traces are given off and pass to them

(Text-fig. 2D; Pl. **1**, fig. 7). Just above this point a few resin canals appear in the abaxial sclerenchyma (Text-fig. 2E) and eventually in the thickest part of the scale there are three distinct series of canals (Text-fig. 2F), the central series alternate with the vascular bundles and the last vestiges of the abaxial sclerenchyma lie between the two outer series.

Anatomy of the seed. The integument is differentiated into three layers of which the sclerotesta, 0·04 cm. thick, is the best preserved (Text-fig. 1B). Internal to this is a very thin layer from which the megaspore membrane has separated by shrinkage in many of the seeds (Text-fig. 1A). The outer layer is very badly preserved and its decay has produced the very irregular surface of the seeds. Abundant resin cavities in the margin of the sclerotesta are present, mainly in the micropylar region whilst at the chalazal end a seed trace is present (Text-fig. 1B). The, presumably, parenchymatous cells in this region have decayed and only a thin outer layer remains which is continuous with the wing on the ascending part of the seed-scale. In some of the seeds an embryo is visible lying in the endosperm (Pl. **1**, fig. 5).



Text-fig. 2. *Pityostrobus leckenbyi.* A–F, An ascending series of transverse sections of the seed-scale complex. *c*, cortex of the cone axis; *d*, decayed chalazal tissue; *r*, resin canal; *st*, seed trace; *v*, vascular bundle. (Camera lucida drawings from cellulose peels off the type specimen.)

Pityostrobus leckenbyi (Carruthers) Seward

Synonymy

Pinites leckenbyi Carruthers, 1869, p. 2, pl. i, figs. 1–5.
Cedrus leckenbyi (Schimper, 1870, p. 299).
Pinites leckenbyi (Gardner, 1886, p. 246).
Cedrus oblonga (Fliche, 1896, p. 200, pl. viii, figs. 1–5).
Cedrostrobus leckenbyi (Stopes, 1915, p. 143).
Pityostrobus leckenbyi (Seward, 1919, p. 385).

Emended specific diagnosis

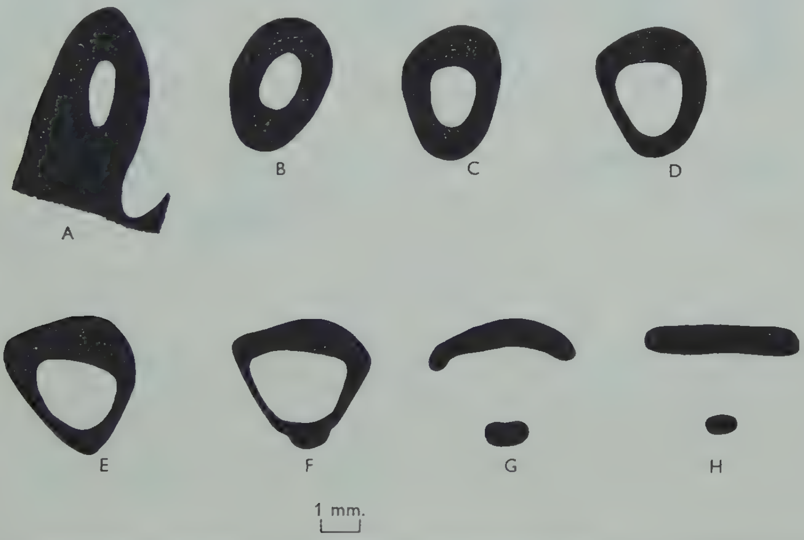
Abietaceous cone, typically ovate in shape but some specimens ellipsoidal. Length 6·5–12·5 cm. and diameter 3·6–5·0 cm. *Bract-scales* small, the free part 0·2 cm. long, with two resin canals. *Seed-scales* spirally arranged and closely imbricated. Horizontal portion 1 cm. long, ascending portion 2·3 cm. long. Exposed apical area 2·8 cm. by 0·4 cm., minutely striated. *Seeds*, winged, 0·9 cm. long and 0·4 cm. in diameter; sclerotesta 0·04 cm. thick; resin cavities in the outer layer of the integument mainly in the micropylar region. *Vascular supply* to the seed-scale and bract-scale united at first into a cylinder, 0·33 cm. by 0·25 cm. in cross-section, giving rise to a rounded bract trace and a flat seed-scale strand; single row of rounded vascular bundles in the upper part of the seed-scale; three resin canals in the base of the seed-scale, two lateral to the trace and one adaxial to it; three series of canals in the upper part of the seed-scale, one close to the abaxial surface, one close to the adaxial surface and one alternating with the vascular bundles; no resin canals in the abaxial sclerenchyma at the base of the seed-scale.

Type specimen. Cone with mounted cellulose peels in the Collection of the Sedgwick museum, Cambridge. Horizon: Lower Greensand. Locality: Shanklin, Isle of Wight; K 2216.

Other specimens. Cones with mounted cellulose peels in the Collection of the Ecole Nationale Supérieure de Géologie Appliquée, Nancy, France. Horizon: Albian-Cenomanian. Locality: Clermont en Argonne.

DESCRIPTION OF *PITYOSTROBUS OBLONGUS*

The type specimen, a water-worn cone from the Upper Greensand of the Dorset coast, is 6·75 cm. long and 3·0 cm. in diameter at the widest point. Clearly the specimen was originally much longer as there are incomplete seeds at both the base and the apex; judging by the general shape of the axis and basal portions of the scales the outward shape of the cone might well have been ellipsoidal or even cylindrical rather than ovate.

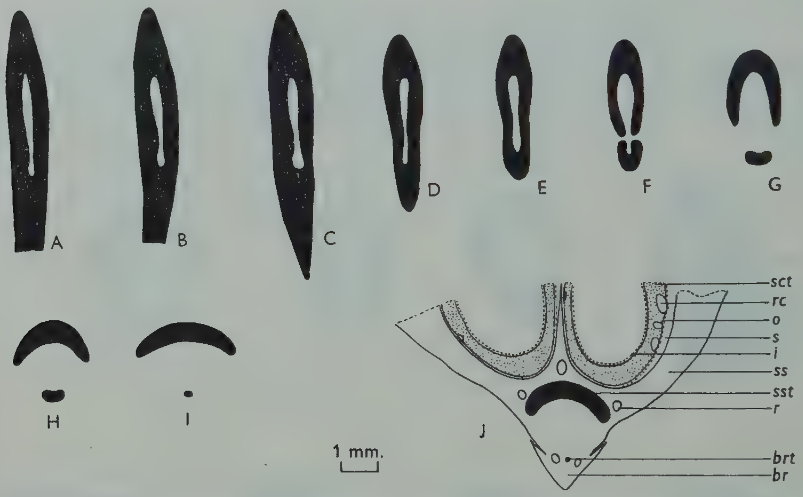


Text-fig. 3. *Pityostrobus leckenbyi*. A–H, A series of transverse sections of the vascular supply to the seed-scale complex and bract-scale, showing the development of the independent traces from the combined cylinder that arises from the stele of the cone axis.

When this specimen was originally described it had been cut down the median vertical plane and the two halves were figured by Lindley & Hutton (1835), these figures are also to be found in Seward (1919). For the purposes of this description cellulose peels were taken from one of the cut surfaces, so as to reveal more of the internal anatomy.

The axis is relatively slender, being 0·6 cm. wide at the base of the specimen and tapering slightly to 0·45 cm. at the apex. The pith is 0·25 cm. wide at the base and 0·15 cm. at the apex. The angles between the scales and the axis are about 80 degrees, none of the scales is set obtusely, but near the apex some are more acutely arranged. The complete bract-scale is 0·45 cm. long, it is partly fused to the seed-scale complex, but its lateral margins become free shortly after leaving the axis (Text-fig. 4J) and about 0·15 cm. of the tip is completely free. The rhomboidal zone of attachment to the axis of the fused bract and seed-scale is 0·5 cm. high and 0·4 cm. wide. The basal portion of the seed-scale is 0·2 cm. thick and this decreases to 0·1 cm. in the chalazal region of the seeds. There are two winged seeds on each seed-scale; the ellipsoidal sclerotesta of each is 0·5 cm. long and 0·25 cm. wide.

The vascular supply to the seed-scale complex and bract-scale leaves the axial vascular system as a combined cylindrical trace appearing in cross-section as an elongate ellipse (Text-fig. 4C). A narrow slit-like gap appears first in the axial xylem about 0·3 cm. high and 0·05 cm. wide. As the trace enters the cortex it is 0·65 cm. high and 0·12 cm. wide (Text-fig. 4D), the U-shaped bract trace then separates from the horseshoe-shaped seed-scale trace and the open portions of each tend to close up slightly (Text-fig. 4F; Pl. **1**, fig. 1). However, on entering the fused bases of the bract and seed-scales the bract trace becomes rounded and the seed-scale trace gradually opens out (Text-fig. 4G, H, I; Pl. **1**, fig. 3). The system of cortical resin canals in the axis gives rise to two lateral and a single adaxial resin canals in the base of the seed-scale. Two canals arise independently in the bract-scale. There are no resin canals in the abaxial sclerenchyma in the base of the seed-scale.



Text-fig. 4. *Pityostrobus oblongus.* A–I, A series of transverse sections of the vascular supply to the seed-scale complex and bract-scale, showing the development of the independent traces from the combined cylinder arising from the stele of the cone axis. *J*, A vertical section through the partly fused bases of a seed-scale complex and bract-scale. *br*, bract-scale; *brt*, bract trace; *i*, inner layer of the integument; *o*, outer layer of the integument; *r*, resin canal; *rc*, resin cavity; *s*, space caused by shrinkage of the sclerostesta; *sct*, sclerotesta; *ss*, seed-scale complex; *sst*, seed-scale complex trace. (Camera lucida drawings from cellulose peels off the type specimen.)

The integument of the seed is differentiated into three layers, of which the sclerotesta, 0·025 cm. thick, is the best preserved. Abundant large resin cavities are present in the margin of the sclerotesta, both in the micropylar and chalazal regions (Pl. **1**, fig. 2). The cells in the latter region have largely decayed and often only the thin outer layer remains, occasionally however vestiges of seed traces are discernible.

Pityostrobus oblongus (Lindley & Hutton) Seward.

Synonymy

Abies oblonga Lindley & Hutton, 1835, p. 137, pl. cxxxvii, figs. 1–2.
Elate oblonga (Unger, 1845, p. 199).
Pinites oblonga (Endlicher, 1847, p. 20).
Pinites oblongus (Unger, 1850, p. 358).
Abietites oblongus (Goeppert, 1850, p. 207).
Pinites oblongus (Carruthers, 1866, vol. 3, p. 541; 1867, vol. 5, p. 12).
Abietites oblongus (Gardner, 1886, p. 246).
Pinites oblongus (Williamson, 1887, p. 189, p. ix, figs. 1–2).
Pinostrobus oblongus (Stopes, 1915, p. 135).
Pityostrobus oblongus (Seward, 1919, p. 387).

Emended specific diagnosis

Abietaceous cone, incomplete but probably originally 8–9 cm. long and 3·0 cm. in diameter, cylindrical; axis, 0·45 cm.–0·6 cm. in diameter. *Bract-scale* small, the free part 0·15 cm. long. *Seeds*, winged, 0·5 cm. long and 0·25 cm. wide; sclerotesta 0·025 cm. thick; resin cavities throughout the outer layer of the integument. *Vascular supply* to the seed-scale and bract-scale united at first into a cylinder 0·65 cm. by 0·12 cm. in cross-section, eventually giving rise to a U-shaped bract trace and a horseshoe-shaped seed-scale strand. *Resin canals*, three in number, in the base of the seed-scale, two lateral to the trace and one adaxial to it; two canals in the bract-scale lateral to the trace.

Type specimen. Cone, in two portions O.U.M. K 10a and O.U.M. K 10b, with mounted cellulose peels, O.U.M. K 10b/P 1–14, in the Department of Geology and Mineralogy, University Museum, Oxford. Horizon: Upper Greensand. Locality: Lyme Regis.

Discussion

Clearly emerging from this investigation is the fact that those who believed Fliche's cones to belong to *Pityostrobus leckenbyi* were correct, but, on the other hand, they were not correct in assuming any special relationship to the modern genus *Cedrus*. Those who believed *Pityostrobus oblongus* and *P. leckenbyi* to be conspecific had a fairly broad, but not excessive, view of the latitude of a species. Finally those who held that *P. oblongus* had fundamental resemblance to cones of the genus *Pinus* are shown to have been in error.

There are of course many points of resemblance between *Pityostrobus oblongus* and *P. leckenbyi*, but there are also points of difference and these are important enough to justify the maintenance of the individual specific names. The differences are concerned with the vascular supply to the seed-scale and bract-scale, with the form of the axis and with the relative distribution of resin cavities in the seeds. In the case of *P. oblongus* the combined trace divides to form two traces, one U-shaped and the other horseshoe-shaped, whereas in *P. leckenbyi* the seed-scale trace appears as an almost flat band when it has finally separated from the bract-scale trace. The form of the axis of *P. oblongus* is much more cylindrical than that of *P. leckenbyi*, which tends to be considerably wider at the base. The seeds of *P. oblongus* have abundant resin cavities distributed throughout the outer layer of the integument, but those of *P. leckenbyi* have them chiefly in the vicinity of the micropyle. These differences are not really within the limits of intraspecific variation, and therefore *P. oblongus* and *P. leckenbyi* are maintained as separate species.

The problem of attempting to establish the affinities of an Abietaceous fossil cone by comparison with the anatomy of modern ones has been very thoroughly studied by Alvin (1953, 1957). He has extended the work of Jeffrey (1905), who recognized two sections, the Pineae and the Abieteae, in the Abietaceae. In the Pineae (*Pinus*, *Picea*, *Larix* and *Pseudotsuga*) resin canals are present in the cortex, the seed-scales are persistent, resin cavities are absent from the integument and there are no vascular traces to the seeds. In the Abieteae (*Tusga*, *Abies*, *Cedrus*, *Keteleeria* and *Pseudolarix*) resin canals are absent from the secondary xylem (except in *Abies*), the seed-scales are deciduous (except in *Tsuga* and *Keteleeria*), resin cavities are present in the integument and seed traces are found.

Pityostrobus leckenbyi and *P. oblongus* cannot be placed satisfactorily in either of Jeffrey's sections as they possess some of the features of each. They resemble the Pineae in that they have cortical resin canals and their seed-scales were almost certainly persistent. They resemble the Abieteae in that they have traces to the seeds, resin cavities in the integument and the distribution of resin canals in the base of the seed-scale is adaxial. On balance they appear to be more allied to the Abieteae than to the Pineae, and the suggestion that *P. oblongus* is an abraded cone of a member of the Pineae now seems most unlikely in view of its anatomical structure. Resemblance of *P. leckenbyi* to the cones of the genus *Cedrus* is purely in the external form; there is a striking similarity, although the apical pit of a typical *Cedrus* cone is absent. Internally most of the structural anatomy has a greater resemblance to that of a cone of *Abies* or *Picea* than to *Cedrus*, the cone structure of which is highly specialized.

Acknowledgements

I wish to express my grateful thanks to the Director of the Ecole Nationale Supérieure de Géologie Appliquée (Université de Nancy) for his kind permission to borrow and section the figured specimens of *Pityostrobus leckenbyi*. I am indebted to the Curator of the Sedgwick Museum, Cambridge, for the loan of the type specimen of *P. leckenbyi* and to the Curator of the Geological Collections of the University Museum, Oxford, for the loan of the type specimen of *P. oblongus*. I am very grateful to the Keeper of Geology, British Museum (Natural History), for arranging for the loan of the specimens. Thanks are due to the Research Fund of the University of London for a grant to purchase large slides and cover glasses for the mounting of the cellulose peels. I wish also to record my gratitude to Mr P. R. Bell of University College, London, and to Dr K. L. Alvin of Imperial College of Science and Technology for advice during the investigation and for very helpfully criticizing the manuscript.

Summary

An account is given of hitherto unpublished details of the anatomy of the type specimen of *Pityostrobus leckenbyi* (Carruthers) Seward, and of two similar cones from the Albian-Cenomanian of France. A comparison is made with *P. oblongus* (Lindley & Hutton) Seward, and reasons are given for maintaining these as separate species.

Addendum

At the time of going to press the author's attention was drawn to the fact that an account by Mlle. Christiane Lauvel of some more of Fliche's specimens from the Museum at Nancy was shortly to appear under the original name of *Cedrus oblonga* in the Comptes Rendues de la Société Géologique de France.

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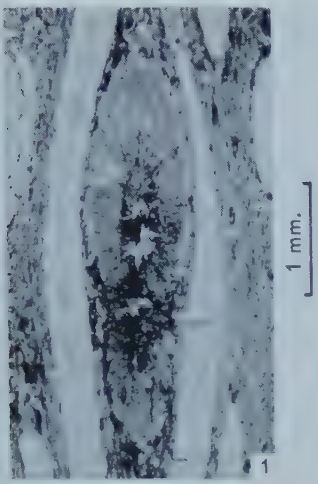

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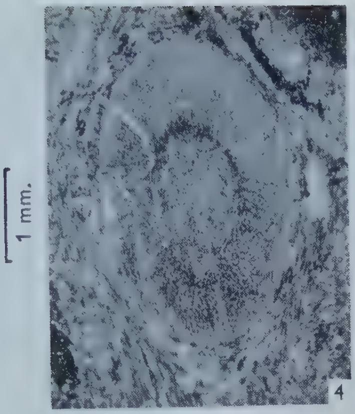

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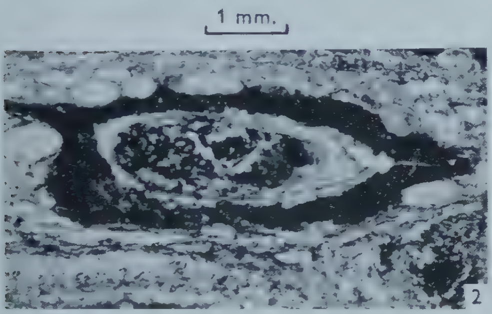

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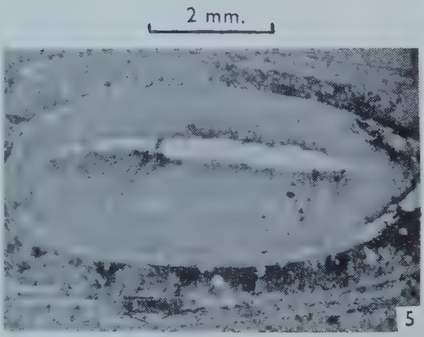

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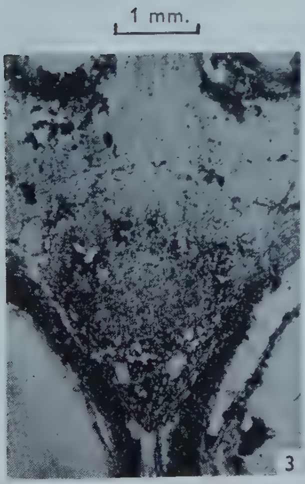

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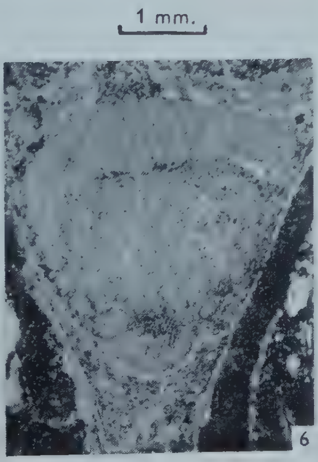

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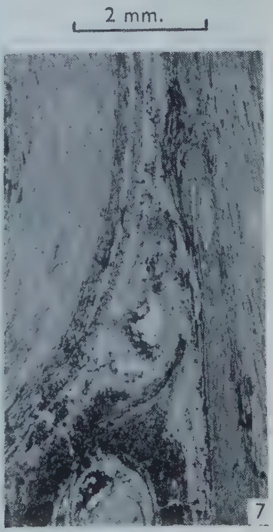

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EXPLANATION OF PLATE

Figs. 1–3. *Pityostrobus oblongus*

Fig. 1. A transverse section of a pair of seed-scale and bract traces; two cortical resin canals are shown cut longitudinally.

Fig. 2. A longitudinal section of a seed showing the abundant resin cavities in the outer integument.

Fig. 3. A transverse section through the fused bases of a seed-scale and its bract-scale.

Figs. 4–7. *Pityostrobus leckenbyi*

Fig. 4. A transverse section through a combined seed-scale and bract trace.

Fig. 5. A longitudinal section of a seed showing an embryo lying within the endosperm; to the left are the closely appressed cotyledons and the radicle is to the right.

Fig. 6. A transverse section of a seed-scale trace and a bract trace at the point of separation.

Fig. 7. A longitudinal section of the chalazal region of a seed showing a seed trace diverging from the vascular tissue of the seed-scale and entering the sclerotesta.

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Dactylis marina Borrill, sp.nov., a natural group of related tetraploid forms

By MARTIN BORRILL, Ph.D., F.L.S.
Welsh Plant Breeding Station, Aberystwyth

INTRODUCTION

Dactylis is a genus of the Gramineae which has recently attracted the attention of a number of investigators. The taxonomist Domin, in particular, came to possess an intimate knowledge of a very wide range of material, based on studies in herbaria, and in the field; this resulted in a monograph (Domin, 1943) recognizing one species, *D. glomerata* L. and eight subspecies.

Cytological studies have shown that two chromosome numbers occur, diploid, $2n = 14$, and tetraploid, $2n = 28$. The first diploid reported, *D. aschersoniana* Graebn., was investigated extensively by Müntzing (1937), and subsequent research, notably by Zohary, has revealed an additional ten or more diploid forms. The diploids possess distinctive morphological and physiological characteristics, occur in particular geographical areas, and have therefore been regarded as subspecies by Stebbins & Zohary (1959).

Dactylis is widely distributed in temperate regions, and over most of this area occurs as tetraploid forms, some of which may simulate one or other of the diploids very closely. In some regions diploid and tetraploid may grow together in the same habitat. The tetraploid complex is very confusing to the taxonomist because the numerous interfertile forms are continuously distributed, providing opportunities for natural hybridization followed by introgression.

In an ideal classification of the diploids and tetraploids one would be justified in considering as a species, any natural group showing clear evidence of relationship by virtue of a distinct eco-geographical distribution, and characteristic phenotype. The tetraploid subspecies recognized by Domin are characterized by one feature, the lobed lemma apex, which is present in subsp. *hispanica* (Roth) Nym. and absent from subsp. *glomerata* Hayek. At present it is not clear whether this is a stable taxonomic character indicative of affinity, or one which is liable to be modified by the selective influence of the environment, and consequently their status as natural groups is uncertain (Borrill, 1961).

Subspecies *hispanica* itself contains the numerous geographical races of the Mediterranean region, one of which, var. *hackelii* Aschers. & Graebn. is easily recognized because of the presence of epidermal papillae (Borrill, 1956). A survey has been carried out of the forms having this feature in common, and the results, presented in this paper, show that they are a natural group which should be separated from subsp. *hispanica* and for which the name *D. marina* is proposed.

MATERIAL AND METHODS

The material examined consisted of living population samples from a wide range of habitats in northern Europe and the Mediterranean region; of these 210 were tetraploid and 12 diploid. When sufficient experience had been gained the study was extended to include *Dactylis* specimens in the herbaria at Kew and the British Museum (Nat. Hist.). Populations allied to var. *hackelii* were found in nineteen localities, particulars of those studied in detail, together with a normal epidermal form subsp. *hispanica* Bc 3959, and the diploid *D. smithii*, are given in Table 1.

In order to produce sheets of epidermal cells for study, the following procedure was adopted. Leaves which had reached maturity were killed by immersion for 5 min. in boiling water, then decolorized by boiling in 70 % alcohol, cleared in hot lactic acid, and finally transferred to cold lactic acid. When herbarium specimens were used they were

Table 1. Dactylis *material studied*

Accession number	Locality	Habitat		Collector
		Tetraploid		
Dactylis marina Borrill:				
Bc 3932	A. South-east France, Le Trayas	Abundant on stony, porphyritic slopes by sea cliffs in open degraded maquis, with *Pinus* and *Myrtus*		J. P. M. Brenan, Kew Herbarium, 21. v. 1950
Bc 4296	B. Portugal, Estremadura province, Nazare	In maritime pasture		Estaçao Agronomica Naçional, Sacavem, 10. viii 1951
Bc 4605 (FAO 3600)	Portugal, Estremadura province, Nazare	Numerous small plants on cliff side above ocean, in brown loam over limestone		F.A.O., 18. viii. 1954
Bc 4782	D. Portugal, Estremadura province, Sintra, in Praia Grande near Collares	In maritime pasture by riverside		A. R. Pinto da Silva, Estaçao Agronomica Naçional, Sacavem, vii. 1957
Bc 4431	E. Portugal, Estremadura province, Sintra, in Praia des Maças	By the sea-shore		Estaçao Agronomica Naçional, Sacavem, 1. x. 1957
Bc 4433	F. Portugal, Estremadura province, Sintra, Azenhas do Mar	—		G. L. Stebbins, Berkeley, California, 1. x. 1956
Herb. British Museum	Portugal, Island of Berlenga	—		A. A. de Carvalho Monteiro, 1884
Herb. Kew	G. Libya, west of Derna towards Res el Hilal	On stony wastes by the sea		Expedition to Libya, 1939
Herb. Kew	Canary Islands, Ribera de Junella	Sea-cliffs		R. T. Lowe, 12. vii. 1855
D. marina hybrids:				
Bc 4430	J. Majorca, San Vincente	On the sandy sea-shore		J. W. Gregor, Scottish Plant Breeding Station, Pentlandfield, Roslin, Midlothian, 1. x. 1956
Bc 4126	C. Morocco, 21 km. from Tangier	In xerophytic vegetation by the sea		A. Money-Kyrle, 21. ix. 1952
D. glomerata subsp. *hispanica* (Roth) Nym.:				
Bc 3959	K. Portugal, Estremadura province, Sintra	—		Estaçao Agronomica, Naçional, Sacavem, 1. ii. 1951
		Diploid		
D. smithii Link:				
Herb. Kew (primary head)	Canary Islands, Palma, Caldera, el Capadero	On cliff	In dry mostly shady crevices in volcanic rock at altitudes ranging between 150 and 600 m.	T. A. Sprague & J. Hutchinson, 13. vi. 1913
Herb. Kew (secondary heads)	L. Canary Islands, Teneriffe, Baxamar	In a rocky place		E. Bourgeau, 14. v. 1855

given a preliminary soaking in water plus a wetting agent, and the period in hot lactic acid was extended. When satisfactorily cleared and softened, a suitable length of leaf was placed adaxial surface downwards on a tile and all the tissue except the upper epidermis then scraped away with a scalpel. The resulting sheet of cells was inverted, placed in cotton blue which stains the guard cells and papillae, and mounted in lactic acid. Pieces of treated epidermis can be kept in this manner for at least 6 months. This technique demonstrated the papillae in fresh material very well, as shown in Pl. 1 and 2. In the case of herbarium specimens (G), they are not quite so clearly seen. A full account of this method is given by Clarke (1960).

THE LEAF EPIDERMIS

The structure of the leaf epidermis was analysed in detail in ten tetraploid populations and the results are illustrated in three ways, by epidermal strips in Pl. 1 and 2, and by sections of the epidermis in Pl. 3. The material falls into three groups: (1) with papillose epidermis, (2) with normal epidermis, (3) intermediate forms. The main differences between these can be summarized as follows:

Epidermal type ...	Papillose	Intermediate	Normal
Percentage cells with papillae	91–100	3–53	0
Cell length	6·85–11·20	9·38–14·53	21·48
Cell shape (ratio: length/width)	1·24– 2·99	2·78– 5·06	6·22

In the papillose type, which included the five populations A, B, D, E and G, the outer wall of nearly every cell is inflated into a more or less subspherical protuberance, the form of which is clearly visible in the transverse and longitudinal sections in Pl. 3*a* and *b*. In surface view the leaf when magnified forty times appears to be covered by globules, Pl. 1 A*a*, B*a*, and the shortness of the cells and high frequency of papilla production is evident in the epidermal strips. The outline of the longitudinal walls in a cell row is markedly sinuous, each cell having a median bulge corresponding with the position of a papilla. The facility with which the papillae stain in cotton blue is shown in the enlargement, Pl. 2 I.

The normal form of epidermis represented by a population of subsp. *hispanica* from Sintra, K, is the antithesis of that just described. The shape of the cells can be seen in section in Pl. 3*c* and *d*. They are much longer, and completely devoid of papillae. In surface view the appearance of this type of epidermis is quite distinct, the whitish dots being stomata (Pl. 2 K*a*, *b*). There is no difficulty in separating var. *hackelii* forms from the general run of *Dactylis* diploids and tetraploids which have the normal epidermal type.

Two of the wild populations examined, Tangier, C, and Majorca, J, were intermediate in cell characters, the former having few papillae, and markedly hexagonal cells (Pl. 1 C*a*, *b*), the latter having somewhat protuberant outer cell walls, as seen in section (Pl. 3*e*, *f*), and in surface view (Pl. 2 J*a*). These are, however, not sufficiently prominent to show up as papillae in the epidermal strip. The walls of the longitudinal cell rows are somewhat sinuous.

Genetical studies, the results of which will form the subject of a further paper, suggest that papilla production is under polygenic control. A large number of F_1 hybrids have been obtained between papillose and normal types, and from progeny to progeny there are large differences in average phenotype, the range of which exceeds the variation shown in these natural intermediate populations suggesting that they have a hybrid ancestry. The epidermis of one of the progeny from a cross between a papillose plant from Nazare, B, and a normal type from Sintra, K, is shown in Pl. 2 H, where it can be compared with the epidermal strips of the parents, and of the intermediate forms. In

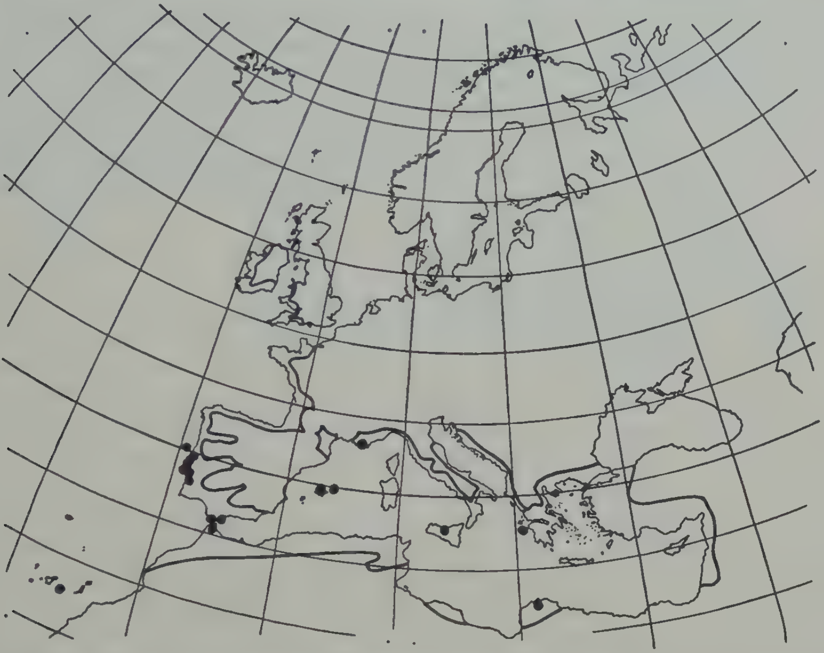
Table 2. *Epidermal cell characteristics*

(Dimensions in μ.)

Population	Accession no.	Cell length	Cell median	Width end	Cell-shape		Papilla diameter	Stomatal length	Stomata per unit area	Cells per unit area	Papillae per unit area	% cells with papillae
					$\frac{\text{Length}}{\text{width}}$	$\frac{\text{Median width}}{\text{end width}}$						
A*a*, *b*	Bc 3932	117·2	41·2	10·6	2·83	2·51	42·7	47·3	65	129	123	95
B*a*, *b* and I	Bc 4296	68·5	55·0	35·9	1·24	1·53	40·5	49·3	62	167	167	100
C*a*, *b*	Bc 4126	145·3	28·7	8·8	5·06	3·26	23·1	34·9	132	171	6	3
D	Bc 4782	90·3	46·6	20·0	1·93	2·32	32·1	40·6	72	179	170	94
E	Bc 4431	104·2	34·8	19·9	2·99	1·74	29·2	44·3	72	130	123	94
F	Bc 4433	93·8	33·6	20·9	2·78	1·60	27·8	43·6	112	172	92	53
G	Libyan (Herb. Kew.)	87·0	50·4	28·2	1·72	1·78	43·0	37·6	72	180	164	91
H	Hybrid	130·7	31·9	18·8	4·09	1·70	28·7	46·2	71	143	71	49
J*a*, *b*	Bc 4430	132·7	37·1	18·2	3·57	2·03	—	45·7	57	189	—	—
K*a*, *b*	Bc 3959	214·8	34·4	15·9	6·22	2·15	—	46·0	62	124	—	—
L*a*, *b*	*D. smithii* (Herb. Kew.)	86·8	23·3	14·1	3·71	1·65	28·9	27·9	119	247	2	0·8

this artificial hybrid 49% of the cells have papillae, and the longitudinal walls are sinuous.

The epidermis of all the diploids available has been examined and one, *D. smithii* from the Canary Islands, resembles var. *hackelii* because the walls of the longitudinal cell rows are somewhat sinuous, and some of the cells have papillae (Pl. 2 L*a*, *b*). The stomata and cells in this diploid are much smaller than in the tetraploids.



Text-fig. 1. Distribution of the material of *Dactylis marina* and hybrids included in this study. Coastal areas having a mean January rainfall in excess of 2 in. and air temperature of over 40° F., outlined; ● = recorded distribution of *D. marina*.

DISTRIBUTION AND NOMENCLATURE

During the course of the survey it became clear that all the specimens having a papillose epidermis are generally similar in phenotype, and occupy maritime habitats often on calcareous soils. The chromosome number $2n = 28$ has been found in five collections, and it is very probable that all are tetraploid. This epidermal character, which extends to nearly all parts of the plant, enables plants to be identified easily and possible hybrid forms recognized. These papillose forms can thus be regarded as a related group and classified together.

The name var. *hackelii* has been given to material of this type from coastal sands, maritime pasture, and sea cliffs in Portugal; but it is now clear that there is a much wider distribution of these papillose forms, living plants or herbarium specimens having been seen from Portugal; southern coast of Spain; south-east France; the islands of Minorca, Sicily and Cephalonia; Libya, Tangier; and the Canary Islands (Text-fig. 1). In addition, this variety treated as a form was recognized in France from 'sables maritimes du midi', by Rouy (*Flore de France*, **14**, 287, 1913); and on the north-west African coasts by Maire (*Flore de l'Afrique du Nord*, 3, 68, 1955). Hybrids have been found on Majorca, and in Morocco.

The distribution so far recorded lies in coastal areas with a mean January rainfall of over 2 in., and air temperature in excess of 40° F. Within these limits this grass is apparently most abundant in regions of high summer temperature, and is primarily 'Mediterranean', but this does not preclude a considerable Atlantic extension of its distribution, perhaps comparable to that of *Arbutus unedo* recorded by Sealy (1949). In cultivation at Aberystwyth, the plants were found to thrive and reproduce by seed in a normal way. Outdoors, all individuals survived a ground temperature of 7° F. in February 1956; a year in which between January and March more than 10° of frost were recorded at ground level on 47 days.

It is necessary to decide to what extent the varietal name applies to this widely distributed material. The varietal epithet *hackelii* was chosen by Ascherson and Graebner (*Syn. Mitteleurop. Flora*, **2**, Abt. 1, 380, 1900) instead of *maritima* because *Dactylis glomerata* L. var. *maritima* (Hack.) Richt. (*Pl. Europ*. **1**, 81, 1890), based on *D. hispanica* Roth var. *maritima* Hack. (*Cat. Gram. Port*. p. 23, 1880), is a later homonym and thus illegitimate on account of the validly published *D. glomerata* var. *maritima* Hallier (*Bot. Zeit*. **21**, Beil., *Aufz. Flora Helgol*. p. 7, 1863). Botanically, Hallier's variety is an entity separate from that of Hackel.

Var. *hackelii* Aschers. & Graebn. was based on var. *maritima* Hack. described as follows by Hackel (translation from the French):

'Culms short, 15 cm.; rhizomes sometimes partly creeping; leaves glaucous, folded; panicle very short, 15 mm., ovoid, not lobed; lemma very shortly mucronate'. The specimens cited are in Wilkomm's Herbarium at Coimbra and were collected by Welwitsch at Buarcos, Cabo Mondego and Praia d'Obidos on the Portuguese coast. A specimen in A. Kneucker (Gramin. Exsicc. XII Lieferung, 1903, no. 351) from the Portuguese coast between Buarcos and Figuera da Foz, has been described more fully by Domin (1943) as follows (translation from the Latin):

'There is no creeping rhizome properly speaking, but a prostrate culm, ascending in a curve from a very short base. The plant is about 10–20 cm. high; leaves folded; stem leaves fairly flattened; spikelets 3–4-flowered, ovate, about 5 mm. in length; glumes ovate, short, rather rigid, somewhat shining, obtusely biauriculate, emarginate and mucronate, 5-nerved, with nerves sharply marked, rib-like, even those of the paleae. Anthers up to 2·5 mm. long. Variable; with glabrous spikelets and glumes ciliate on the keel.'

When the material outside Portugal is taken into account, the range of phenotypic variation found is considerable, and this might be expected, since a sufficiently varied number of habitats is available in the maritime environment to permit some differentiation into local races. This is exemplified in Pl. 3 by plants of the two extreme populations from Le Trayas (A), and Nazare (B). Grown in fertile soil at Aberystwyth they were generally larger in vegetative growth and panicle size, than the Portuguese specimens described by Hackel, and by Domin. The main differences between these extreme populations are as follows:

		Upper size limit of				
Type of plant	Population	Culm length (cm.)	Panicle length (cm.)	Spikelet length (mm.)	No. of florets per spikelet	Pubescence
Tall, more or less erect	A, Bc 3932	70	10	8	4–6	Keels often hairy
Short, fairly prostrate	B, Bc 4296	40	6	5	3–4	Keels often toothed

Although individuals from these two localities often look dissimilar the main differences are in size, and the plant to plant variation within the populations is very great, so that all the characters intergrade completely, forming a continuous range of variation.

In tetraploid *Dactylis* generally, there is no coherent pattern of variation in floristic characters amongst the complex of geographical races (Borrill, 1961). This situation also occurs in the maritime form because the inflorescence has no diagnostic features separating it from races of subsp. *hispanica*. Fortunately other characters have been found which show that the maritime forms are related. These are: (1) a papillose epidermis; (2) inflated flag-leaf sheaths; (3) a tendency to branching at the basal nodes of the culms. None of these characters was mentioned by Hackel or Domin.

The group exhibits variation in excess of var. *hackelii*, and possesses important features not mentioned in the varietal description. It is therefore proposed to give specific rank to this natural group of related, papillose, tetraploid forms. In selecting a name for the taxon, *maritima* is not available at specific rank on account of the prior occurrence of:

D. maritima Curtis, *Enum. Brit. Gr.* **4**, (1787) = *Spartina stricta*
D. maritima Schrad., *Fl. Germ.* **1**, 313, t. 6, f. 1, = *Aleuropsis laevis*
D. maritima Walt., *F. Carol.* p. 77 (1788) = *Spartina laevigata*

nor at infra-specific rank because of:

D. glomerata var. *maritima* Hallier, *Bot. Zeit.* **21**, Beil., *Aufz. Flora Helgol.* p. 7 (1863); the epithet *hackelii* is available, but I have chosen to discard this, since as originally conceived it applies only to one facet of the papilla-bearing *Dactylis*, and to adopt the name *marina*.

DACTYLIS MARINA Borrill sp.nov.

Synonyms: Non. *D. glomerata* var. *maritima* Hallier, in *Bot. Z.* **21**, Beil., *Aufz. Flora Helgol.* p. 7 (1863).
D. hispanica var. *maritima* Hack., *Cat. Gram. Port.* p. 23 (1880).
D. glomerata var. *maritima* (Hack.) Richt., *Pl. Europ.* **1**, 81 (1890).
D. glomerata var. *hackelii* Aschers. et Graebn., *Syn. Mitteleurop. Flora*, **2**, Abt. 1, 380 (1900).

Plantae parvae, saepius dense caespitosae, paulum prostratae, culmis curvatis adscendentibus nonnunquam erectiores. Culmi (10)20–50(70) cm. longi, *Saepe ramosi, capites secundarios in nodis basilaribus ferentes*, praesertim in autumno. Paniculae saepius breves, plus minusve ovatae, nonnunquam lobatae, rarius longiusculae cum glomerulo paululo disiuncto basilari, (2)4–6(10) cm. longae. Folia plicata, vetera plana, *semper glauca. Vaginae foliorum superiorum plus minusve inflatae. Epidermidis cellulae cum papillis subsphaericis per omnes fere partes subaereas extense.* Spiculae congestae, 4–6(8) mm. longae. Glumae et lemmata brevia, rigidiuscula, paululo nitida, nervis prominentibus, costis similibus. Carinae, praesertim glumarum, inconstanter pubescentes, nonnunquam tantum minute denticulatae. Lemmatum apices emarginati, breviter mucronati.

Hab. In pascuis rupibusque litoreis arenosis.

Small plants, usually densely tillering and somewhat prostrate, with curved ascending culms, occasionally more erect. Culms (10) 20–50(70) cm. long, often branching, bearing secondary heads at the basal nodes, especially in autumn. Panicles generally short, more or less ovate, sometimes lobed; more rarely longer with a somewhat distant basal glomerulus, (2)4–6(10) cm. long. Leaves folded, older leaves flat, *always glaucous. Sheaths of upper culm leaves more or less inflated. Epidermal cells possessing subspherical papillae* extending over nearly all the aerial parts. Spikelets compact 4–6(8) mm. long. Glumes and lemmas short, rather rigid, somewhat shining, with prominent rib-like nerves; keels, especially of the glumes, variably pubescent, sometimes only minutely toothed; lemma apices emarginate, and shortly mucronate.

Portugal: Nazare—brown loam over limestone cliff above ocean, and in maritime pasture; Azenhas do Mar, Collares—maritimes ward at Praia Grande; Sintra—Praia des Maças by the sea-shore (all in cultivation at Aberystwyth); Buarcos—on the coast between Buarcos and Figuera da Foz, Cabo da Roca, Portalegre (all in the Kew Herbarium); Insula Berlenga (in the British Museum Herbarium). Spain: Algeçiras—sandy beach, Gibraltar (both in the Kew Herbarium). South-east France: Le Trayas—on stony porphyritic slopes by sea-cliffs in open degraded maquis with *Pinus* and *Myrtus* (in cultivation at Aberystwyth). Mediterranean islands: Minorca—between Fornels and Cabo Cavalleria in pascuis collinis aridis; Sicily—Palermo, Cephalonia—in pasture towards Hagios Theodoros by the sea (all in the Kew Herbarium). North Africa: Libya—stony wastes by the sea-shore west of Derna towards Res el Hilal. Canary Islands: Gran Canaria—Ribera de Junella on sea-cliffs (both in the Kew Herbarium). Hybrids: Majorca—San Vincente on the sandy seashore; Morocco—Tangier by the sea in xerophytic vegetation (both in cultivation at Aberystwyth).

Typus. Borrill Bc 4296. Holotype in Herbarium Welsh Plant Breeding Station, Aberystwyth: isotope in Kew Herbarium. Ex Nazare Portugal.

DISCUSSION

When considering the evolution of *Dactylis marina* it seems reasonable to suppose that it is descended from a single ancestral group of tetraploids sharing a pool of genes expressed in the phenotype as epidermal papillae. These are not necessary for survival in maritime environments, since *Dactylis* from coastal areas such as those of the British Isles, has a normal epidermis. *D. marina* is physiologically adapted to coastal habitats in regions of high summer temperature such as south-west Europe, the Mediterranean, and the Atlantic islands, to which it is apparently confined. It is in this area that putative diploid ancestors might be found, and *D. smithii* shows unmistakable evidence of relation to *D. marina*.

This diploid occurs in dry, mostly shady, crevices in volcanic rock, often on sea cliffs, in the Canary Islands. The growth habit is unusual, with long (35–95 cm.), multinodal (12–25) nodes, more or less erect or spreading culms which are woody at the base, emerging from loose tufts. They are biennial with secondary branches in the first and second years. The primary culm has a long panicle, the secondary culms bearing short, ovate heads, as shown in Pl. 3C.

The resemblance to *D. marina* is in the branching habit, and in the epidermis, the walls of the longitudinal cell rows being somewhat sinuous, and a proportion of the epidermal cells having papillae, as indicated in Pl. 2L *a* and *b*. It is probable that *D. ibizensis* Gandoger from the Balearic Islands is also an ancestral type since, although it has not so far been found to bear epidermal papillae, the walls of the longitudinal cell rows are sometimes sinuous, and according to Stebbins (personal communication) there is evidence to suggest that F_1 hybrids between *D. ibizensis* and *D. smithii* have a much higher frequency of papillum production than has *D. smithii* alone.

In recent years, there has been an increasing interest in the use of the epidermis in plant classification. Instances of this are the studies by Church (1949) in *Glyceria* and by Sørenson (1953) in *Puccinellia*. The present paper extends the use of epidermal characters to *Dactylis*; showing that, in the tetraploid complex usually classified under the name *hispanica*, within which a grouping of geographical races using floristic features is not yet possible, there exists a natural group of related forms, *Dactylis marina*, whose diploid ancestors, or their close relatives, still occur as island endemics.

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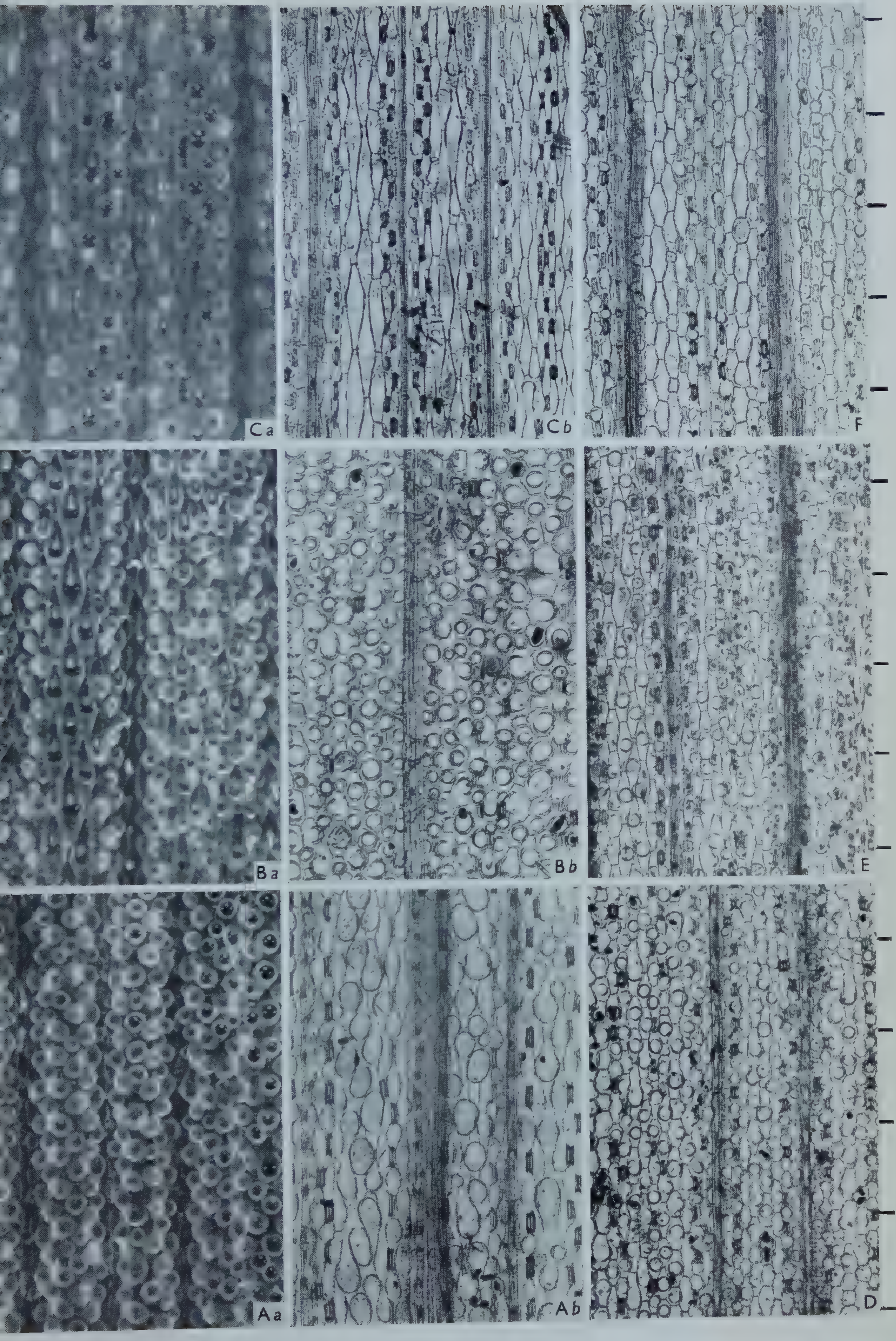
Plate 1



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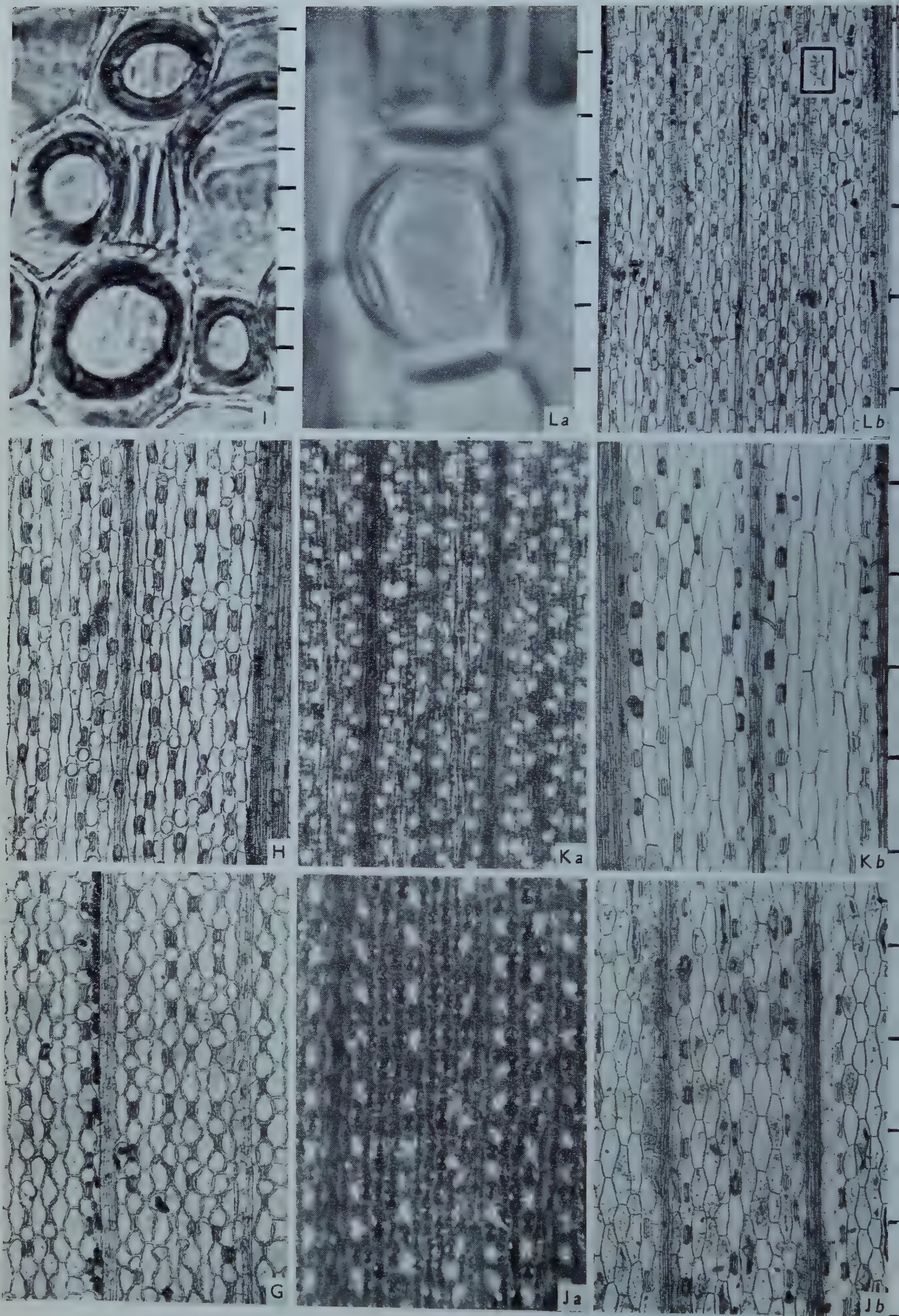

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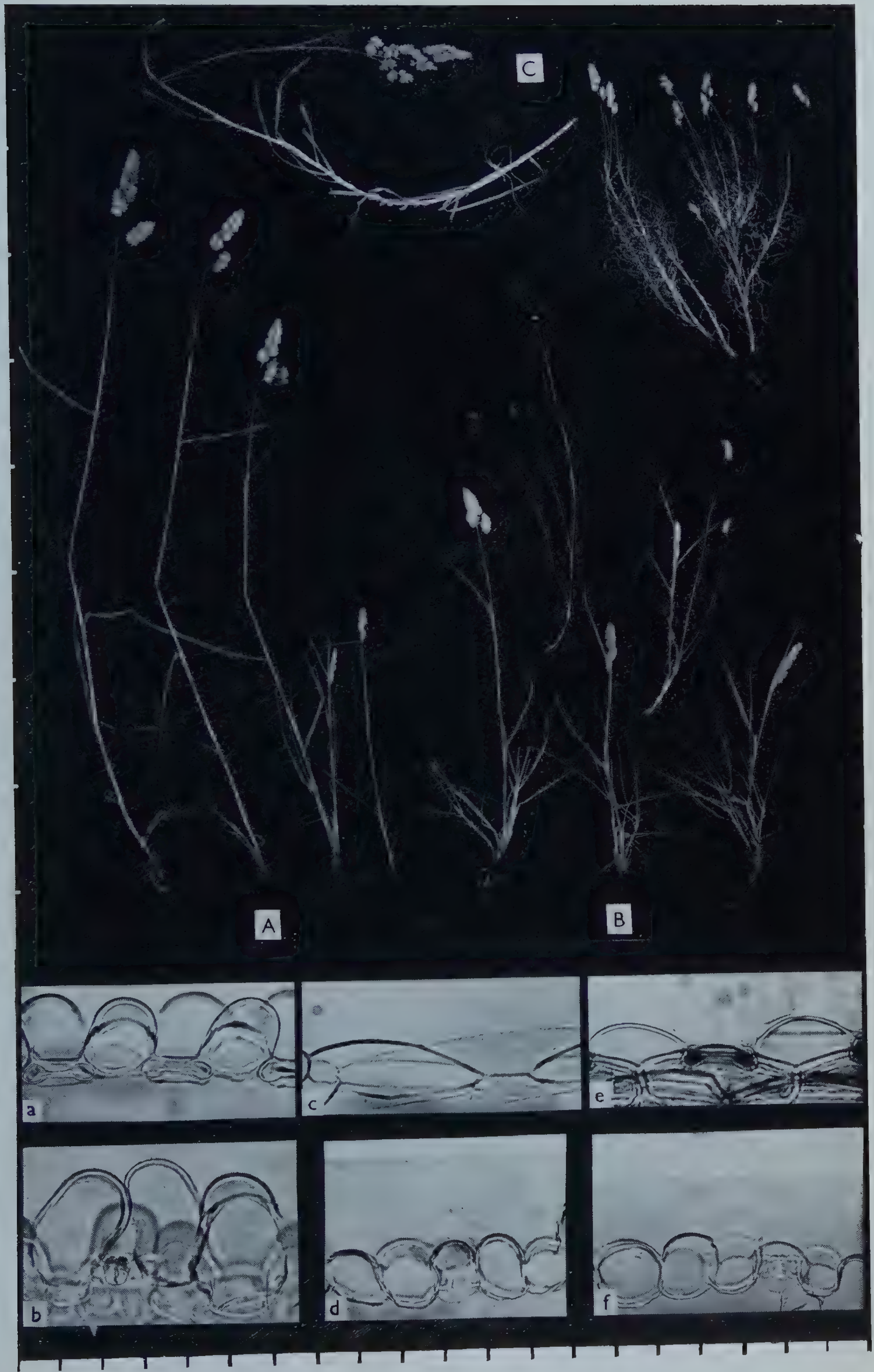

MARTIN BORRILL

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EXPLANATION OF PLATES

Plates 1 and 2

The leaf epidermis in *Dactylis*. 1 division = $200\,\mu$; except in I; and L*a* where 1 division = $10\,\mu$; *a* = incident light, *b* = transmitted light.

A Bc 3932 Le Trayas
B Bc 4296 Nazare
I Bc 4296, Nazare, magnified papillae
C Bc 4126 Morocco (hybrid)
D Bc 4782 Collares
E Bc 4431 Sintra
F Bc 4433 Azenhas do Mar
G —— Libya
H Artificial hybrid, Bc 4296 B, × Bc 3959 K
J Bc 4430, Majorca (hybrid)
K Bc 3959 *D. glom.* subsp. *hispanica*, Sintra
L*a* —— *D. smithii*, single papilla
L*b* —— *D. smithii*, single papilla

Plate 3

Dactylis marina Borrill: A, Le Trayas; B, Nazare.
Dactylis smithii Link.: C, Canary Islands.

$\left.\begin{array}{l}\text{Left: first-year panicle}\\ \text{Right: second-year heads}\end{array}\right\}$ 1 division = 10 cm.

Sections of leaf epidermis: 1 division = $20\,\mu$.
Bc 4296 Population B (*a*) longitudinal; (*b*) transverse.
Bc 3959 Population K (*c*) longitudinal; (*d*) transverse.
Bc 4430 Population J (*e*) longitudinal; (*f*) transverse.

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The pattern of morphological variation in diploid and tetraploid *Dactylis*

By MARTIN BORRILL, Ph.D., F.L.S.
Welsh Plant Breeding Station, Aberystwyth

INTRODUCTION

Those who are familiar with cocksfoot (*Dactylis* L.) as represented by the agricultural varieties grown in Britain must be largely unaware that these are only part of a very variable genus whose component forms are distributed throughout the temperate regions of the world. The species varies in morphology and in chromosome number. It embraces two chromosome types, namely, several partially interfertile diploids, each of limited distribution, and the tetraploids, which are not so confined and represent the species over most of its geographical area.

The main subdivisions of *Dactylis* have been regarded as species by some botanists and as subspecies by others. In this paper the subspecific names proposed by Domin (1943) will be used for the tetraploids. For the diploids, the validly published names are of species rank. Zohary (1956), however, accords subspecific status to all the diploids, and describes three new subspecies *lusitanica*, *judaica* and *santai* to which some of the plants used in this study belong. For convenient reference these names will be adopted, in the expectation that valid publication will not be long delayed (Stebbins & Zohary, 1959).

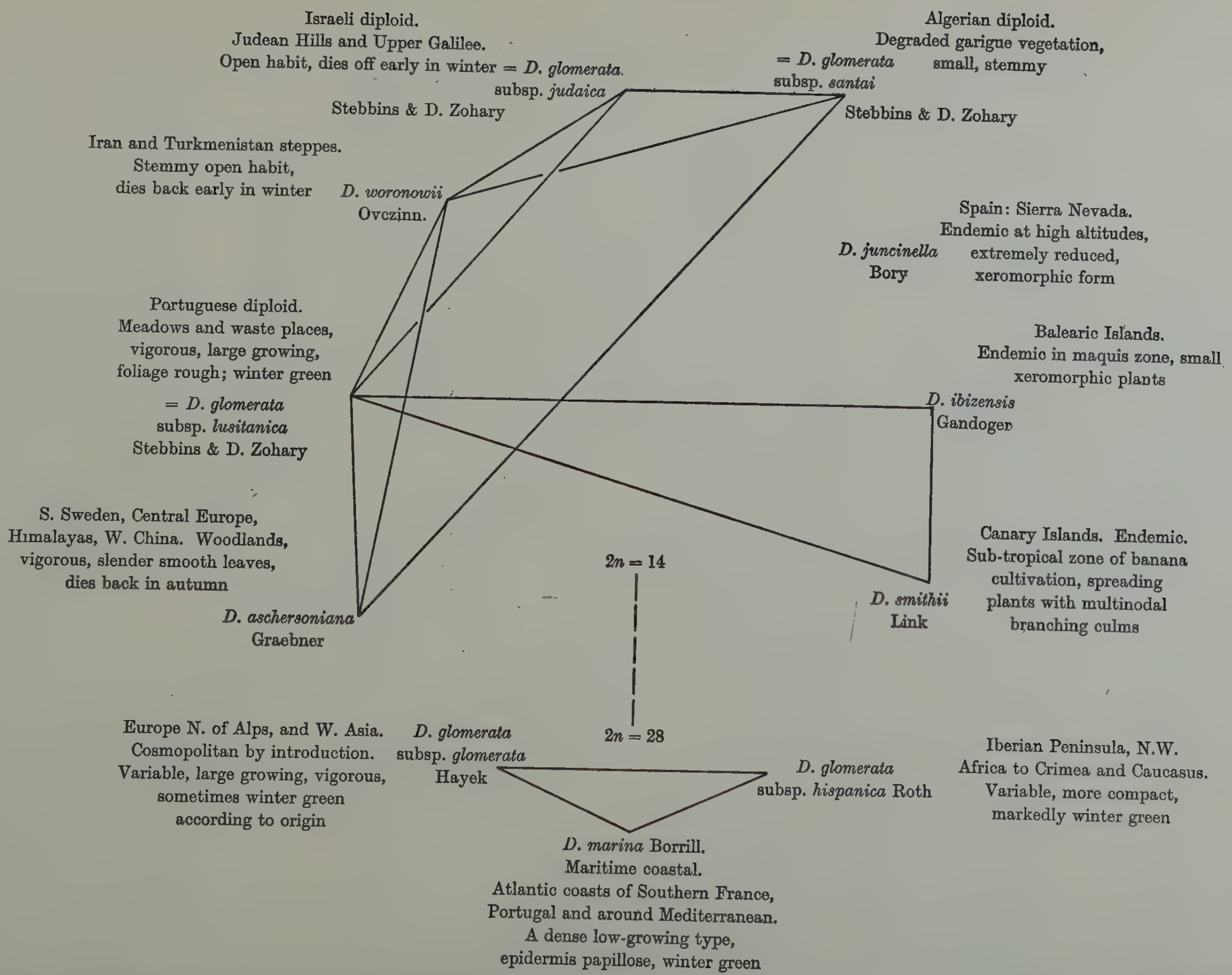
Domin (1943), basing his conclusions on an exhaustive survey of taxonomic and distributional data, and on an intimate personal knowledge of the material, although very few chromosome counts were then available, recognizes a single species of *D. glomerata* and regards the major forms as subspecies amongst which are:

(1) *hispanica* Roth, a xerothermic Mediterranean type including in its limits Ovezinnikov's Asiatic *D. woronowii* which is now known to be diploid. This subspecies extends from the Iberian Peninsula and N.W. Africa to the Crimea and Caucasus, bounded on the north by the Pyrénées, European Alps and Carpathians. It forms an extremely variable complex with only one stable feature, to quote Domin 'the typical subsp. *hispanica* in one form or another has lemmas divided into two blunt lobes from the middle of which grows a very short awnlet, or a mere point which sometimes does not reach the size of an awn.'

This lobed character is most pronounced in plants from the Mediterranean region and becomes less developed in specimens from the northern region which show a transition towards the large growing cocksfoot used in agriculture.

(2) *glomerata* Hayek. This type occurs north of the European Alps, and is well known from its use as a herbage plant. Within its area of distribution it does not appear to have any habitat preferences and has a great capacity for colonization which, aided by the activities of agriculturists, makes it extremely difficult to separate the countries where it originated from those where it is introduced. Domin states that in subsp. *hispanica* he was also able to witness a secondary distribution in the Mediterranean region, on the European and African (Algerian and Moroccan) coasts. This tetraploid complex is very confusing to the taxonomist: the subspecies are interfertile and each contains numerous geographical races which can hybridize freely when brought together.

Text-fig. 1 sets out the main taxa, some of which are shown in Pl. 1, and illustrates the range of variation available in both diploids and tetraploids, their cytological status and capacity for hybridization, which will be considered in detail in a further paper.



Text-fig. 1. Diploid and tetraploid *Dactylis* species and subspecies, with notes on winter growth at Aberystwyth. Crosses attempted: Hybrids fertile, ——— ; hybrids slightly female fertile, — —.

This arrangement should not be regarded as final but rather as a basic scheme subject to modification as our knowledge of the group increases. For instance, among the diploids Zohary regards the forms of *D. aschersoniana* Graebner from the Himalaya and Western China as a separate taxon (*D. glomerata* subsp. *hookeri*), and this paper will show that more than one type occurs in Algeria, one of which is equivalent to Zohary's subsp. *santai*.

Among the tetraploids the maritime variety (Borrill, 1957) is to be regarded as a species (Borrill, 1961). It is quite clear, taking into consideration all the taxa, that there is a great range of variation in this genus.

In this paper Mediterranean and North European tetraploid populations are compared morphologically with one another and with certain of the diploids to see whether any phenotypic trend can be established.

MATERIAL

Populations. Details of the 19 populations studied are given in Table 1. Among the tetraploids 4 belong to the northern subsp. *glomerata*, seven to subsp. *hispanica* and one to *Dactylis marina* Borrill. In the opinion of the collectors the populations used were indigenous. Exceptions were *D. aschersoniana*, and one introduction of *D. woronowii* Ovczinn. which were of botanic garden origin. Furthermore, one has to bear in mind that amongst the northern tetraploids growing in areas where cocksfoot is sown it is always difficult to be sure that introgression has not occurred.

The population from Norway showed positive evidence of being indigenous, in the sense of genetic adaptation to the seasonal requirements at a latitude of 66° N. When the sample was grown at Aberystwyth, all the plants were small and prostrate, and many failed to head. The parent plants were large, vigorous and freely heading.

Measurements. Seedlings of each population were raised in boxes, and in September 1954, 20 were planted in the experimental ground at 2 × 2 ft. spacing without replication. In 1955 nine plants were taken at random from each population sample, the three tallest heads were removed at anthesis, pressed, labelled and stored. The diploids from Algeria and Iran were grown separately and heads collected in 1958. Data were collected for ten gross parts of the panicle, and for seven floristic characters measured on the basal spikelet of the proximal glomerulus. Lemma apex morphology was scaled as described in an earlier paper (Borrill, 1957). Details are given in Table 2. Representative specimens have been placed in the herbarium of the Welsh Plant Breeding Station and duplicate specimens deposited in The Herbarium, Royal Botanic Gardens, Kew.

DIFFERENCES BETWEEN POPULATIONS

Single characters. An analysis of variance was carried out on the fifteen populations grown in 1955, and in Table 2 it may be seen that of the morphological characters selected only two, namely, lemma width and awn length, failed to reach significance. When the means for the various characters are compared with the minimum differences needed for significance at $P < 0{\cdot}01$, it is clear that there are large genetic differences between the populations.

Groups of characters. Correlated changes in phenotype between populations were studied by plotting the means of all characters against one another on scatter diagrams. No trend was observed in the majority of cases; correlation coefficients were calculated for the components which appeared to show some correlation (Table 3). Of these, seven were significant at or above the 5% level, two others, flag leaf: basal pedicel and flag leaf: basal internode just failed to reach significance, probably due to the small number of populations used. Insufficient data were available to include more than five popula-

Table 1. Dactylis *material studied*

Species and subspecies	Chromosome no.	Accession no.	Locality	Habitat	Collector
D. woronowii Ovczinn.					
Iran	14	Bc 4074	—	Botanic Garden, Uppsala, Sweden	—
		Bc 4826(FAO 3697)	Iran	—	F.A.O.
D. glomerata subsp. *santai* Stebbins & D. Zohary (1960)					
Algeria. Algerian diploid but outside the limit of *santai*	14	Bc 4438(FAO 3168)	Relizane	Brown loam, limestone	F.A.O.
		Bc 4439(FAO 3215)	Oued Chiffa	Alluvial loam	F.A.O.
		Bc 4440(FAO 3328)	Bouira	Yellow-brown clay loam	F.A.O.
D. glomerata subsp. *lusitanica* Stebbins & D. Zohary (1960)					
Portugal	14	Bc 3948	Sintra	—	Prof. A. Camara, Estaçao Agronomica Naçional, Sacavem
D. aschersoniana Graebner					
	14	Bc 2835	—	Botanic Garden, Uppsala, Sweden	—
D. glomerata subsp. *hispanica* Roth					
Israel	28	Bc 4155	—	Rendzina soil	Dr Amos Dovret, Gov. Agric. Expt. Stn., Neveh Yaar
		Bc 4156	—		
		Bc 4157	—	—	
Cyprus	—	Bc 4178	—	Limestone formation	Mr K. Jones, Dept. of Agric. Nicosia
		Bc 4179	—	Limestone formation	
		Bc 4180	—	Limestone formation	
Sicily	—	Bc 4062	Palermo	—	Prof. Zanini, Feudo, Giardinella
		Bc 4068	Palermo	—	
Portugal	—	Bc 4291	Azenhas do Mar, Estremadura	In pinewood calcareous soil	Prof. A. Camara, Estaçao Agronomica, Naçional, Sacavem
		Bc 4293	Algueirão, Sintra, Estremadura	Granite soil	
		Bc 4294	Sintra, Estremadura	Dry soil	
		Bc 3959	Sintra	—	
D. marina Borrill					
Portugal	28	Bc 4296	Nazare, Estremadura	Maritime pasture	

Table 1 (*cont.*)

D. glomerata subsp. *glomerata* Hayek					
Scotland	28	Bc 4231	South Queensferry	—	Dr J. Gregor, Scottish P.B.S., Pentlandfield, Midlothian
		Bc 4236		—	
		Bc 4238		—	
Norway	—	Bc 4165	Tjøtta	Station Farm, uncultivated land with bushes and small trees	Dr Magnus Jetne, Staten stamsæd-og, sauealsgard
		Bc 4166			
		Bc 4167			
		Bc 4168			
Finland	—	Bc 4272	Tikkurila	Sandy clay soil	Prof. O. Valle, Agric. Res. Centre, Dep. of Plant Husbandry
		Bc 4273			
		Bc 4274			
Denmark	—	Bc 4141–4	Børkop	Good loamy soil. Uncultivated area between fields and forest	Dr Henrik Bøgh, Pajbjergfonden Overbygaard, Børkop
		Bc 4147–9			
		Bc 4151–4			

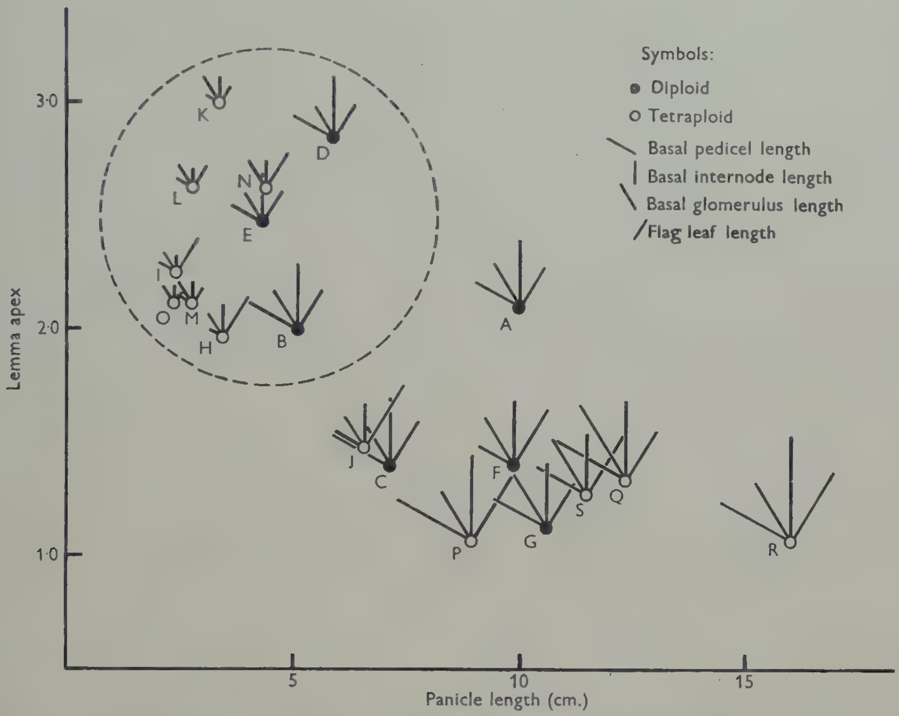
Table 2. *Morphological data, diploids and tetraploids*

Species or subspecies	Origin	Population (Text-fig. 2)	Accession no.	Length (cm.)	Basal internode. Length	Basal pedicel. Length	Basal glomerulus		No. of internodes	Culm internode lengths			Flag leaf length	No. of florets	Length	Lowest spikelet in basal glomerulus lemma of median floret				
							Length	Width		1 (terminal)	2	3				Length	Width	Apex	Awn length	Keel pubescence
D. woronowii	Hortus Uppsala	A	4074	9·96	3·36	2·38	2·37	1·28	11·85	29·85	19·44	10·62	11·30	5·74	7·10	4·72	1·20	2·14	0·70	—
	Iran	B	4826	5·03	3·15	2·57	2·01	—	—	—	—	—	10·48	—	—	5·59	—	2·00	—	—
D. glomerata subsp. *santai*	Algeria	C	4438	7·07	3·23	3·12	1·99	—	—	—	—	—	12·37	—	—	6·44	—	1·40	—	—
		D	4439	5·92	2·90	2·04	1·47	—	—	—	—	—	8·85	—	—	7·41	—	2·85	—	—
		E	4440	4·18	2·17	1·43	1·40	—	—	—	—	—	8·14	—	—	6·42	—	2·48	—	—
D. glomerata subsp. *lusitanica*	Portugal, Sintra	F	3948	9·88	3·12	1·77	2·59	1·46	12·00	24·37	13·77	8·14	16·03	6·11	8·33	6·08	1·11	1·40	0·67	—
D. aschersoniana	Hortus Uppsala	G	2835	10·62	3·11	2·82	3·03	1·70	13·74	25·51	14·62	10·29	11·70	6·14	8·28	6·79	1·04	1·14	0·63	—
D. glomerata subsp. *hispanica*	Israel	H	4156, 7, 8	3·25	1·40	0·40	1·14	1·00	9·51	23·11	17·40	12·14	12·10	4·81	9·14	6·56	1·19	1·96	0·83	3·07
	Cyprus	I	4180, 1, 2	2·37	0·57	0·70	0·77	0·69	6·85	23·40	15·62	7·55	9·30	5·33	8·57	5·97	1·27	2·25	0·48	2·18
	Sicily	J	4062, 8	6·51	2·00	0·90	1·55	0·72	10·96	30·85	16·74	1·30	18·20	4·73	8·06	6·43	1·05	1·48	0·71	3·00
	Azenhas do Mar	K	4291	3·29	1·11	0·45	1·33	1·16	12·03	16·77	11·18	4·81	3·25	6·22	9·39	7·68	1·03	3·00	0·57	1·92
	Portugal	L	4293	2·81	0·66	0·60	1·03	0·92	8·51	27·48	15·48	5·55	5·40	5·59	8·05	6·27	0·97	2·62	0·83	2·66
	Portugal	M	4294	2·66	0·85	0·50	1·00	0·92	9·40	24·81	17·18	6·77	3·10	6·51	8·85	6·50	1·00	2·11	1·01	2·56
	Portugal	N	3959	4·25	1·11	—	1·40	0·75	11·96	32·74	18·07	10·37	9·60	4·59	7·30	5·92	1·23	6·26	0·72	2·74
D. marina	Nazare	O	4296	2·33	0·60	—	0·81	0·84	—	5·59	6·14	6·88	2·44	4·51	6·58	4·32	1·01	2·11	0·37	1·81
D. glomerata subsp. *glomerata*	Denmark	P	4141–4, 4147–9, 4151–4,	8·81	4·21	4·16	2·70	—	—	—	—	—	18·62	—	—	6·40	—	1·07	—	—
	Scotland	Q	4231, 6, 8	12·29	3·96	3·88	4·37	1·16	10·81	40·40	26·14	15·55	14·10	2·85	7·95	6·94	1·15	1·33	0·73	2·63
	Norway	R	4166, 7, 8	15·92	5·34	3·97	3·33	0·94	11·59	30·33	16·74	8·66	19·96	5·03	9·36	6·64	0·92	1·07	0·74	1·59
	Finland	S	4273, 4, 5	11·48	2·95	2·55	3·18	1·23	10·77	27·81	17·62	9·88	18·66	4·44	9·85	8·19	1·07	1·29	0·98	3·14
Significant difference ($P < 0·01$)				4·48	1·895	2·11	1·84	0·492	5·30	13·27	2·25	7·77	7·63	2·07	2·098	0·281	Not sig.	0·321	Not sig.	0·47

tions when making these two comparisons. Panicle length was not related to number of internodes.

Panicle length can be regarded as a key character, and the length of the basal glomerulus and its pedicel, and the length of the basal internode, as related differences in the proportions of the inflorescence.

Panicle length is closely negatively correlated with the lobed condition of the lemma apex, and positively with the length of the flag leaf. Flag leaf and lemma apex show a strong negative correlation.



Text-fig. 2. Correlation diagram. Variation between populations in six phenotypic characters. Key to lettering in Table 2. The broken line indicates the approximate limits of subsp. *hispanica*.

Table 3. *Correlation of characters between populations*

Characters tested	No. of populations	Correlation coefficient
Panicle length		
Basal internode length	13	0·982**
Basal pedicel length	8	0·933**
Basal glomerulus length	14	0·933**
Flag leaf length	11	0·793*
Number of internodes	17	0·580
Lemma apex morphology	19	−0·749**
Flag leaf length		
Basal internode length	5	0·728
Basal pedicel length	5	0·752
Lemma apex morphology	11	−0·851**
Lemma length		
Spikelet length	14	0·856**

* Significant at $P < 0{\cdot}05$; ** Significant at $P < 0{\cdot}01$.

This close relation between panicle length and lemma apex is important because the latter has been regarded as a diagnostic taxonomic character. In a pictorialized scatter diagram of the kind devised by Anderson (1949) (Text-fig. 2) these two characters were used as ordinates. Each population is represented by a glyph, the position of which depends on the dimensions of panicle and lemma apex. The lengths of the radiating arms are proportional to those of basal internode, basal pedicel, basal glomerulus and flag leaf, as shown in the key. On this diagram the trend of variation between populations in these six characters can be studied.

The data show that among the diploids the two groups, *D. woronowii*, and the collection from Algeria, are heterogeneous. Of the two introductions of *woronowii* (A) was from a botanic garden and (B) was seed collected in the field. The former had probably hybridized with another diploid either at Uppsala, or at the Jardin Botanique, Ukraina, from which the material originated in 1938. Caution is needed in using botanic garden material, because of repeated multiplication from seed, and the presence of interfertile forms in the garden, unless there is phenotypic evidence of genetic purity, as in *D. aschersoniana* (G). The original source of the material is unknown.

Among the Algerian collections, (C) is different from (D) and (E), and varies in the direction of the northern diploids. Ecologically the two forms differ:

C. 4438 (F.A.O. 3168). Relizane, 29 km. on road to Zemmora; 350 m. brown loam over limestone south slope of hill, with *Olea*, *Juniperus* and *Pistacia*.
Stebbins 5266. Sidi-bel-Abbès, south side of Mt. Tessala; limestone, in degraded garigue, with *Chamaerops humilis*.
Stebbins 6287. 4 and 5 Djebel Doui, summit south of Duperré, in *Quercus ilex* forest.
Stebbins 5297 Relizane, 30 km. to south-west, on road to Perregaux; limestone, degraded garigue.
D. 4439 (F.A.O. 3215). Oued Chiffa, 400 m. alluvial loam plus some limestone stones, on railway embankment.
E. 4440 (F.A.O. 3328). Bouira, 500 m. yellow-brown clay loam with stones near top of embankment, between road and wheat crop.

It is clear that the material collected within about 50 miles of Sidi-bel-Abbès, at the western end of the Massif de l'Ouarsensis belongs to subsp. *santai* Stebbins & Zohary (1959), whereas the other collection, made in a cultivated area 100 miles away beyond the eastern end of the massif, should be placed in another taxon.

The diploids form a series beginning with the small-growing xerothermic type from eastern Algeria (D) and (E), and the steppe forms from Iran (B), passing via the montane, possibly forest, subsp. *santai* (C) from western Algeria, to the large-growing vigorous subsp. *lusitanica* Stebbins & D. Zohary (1959) of western Portugal (F), and *D. aschersoniana* (G) from the central European forests.

Table 4. *Number of spikelets per panicle in various subspecies*

Species or subspecies	No. of plants	Mean no. of spikelets per panicle	Group
D. woronowii	—	—	—
D. aschersoniana	194	137	A
D. glomerata			
Subsp. *lusitanica*	—	—	—
Subsp. *judaica*	17	84	B
Subsp. *glomerata*	109	126	C
Subsp. *hispanica*	152	74	D

Group AC: BD differs significantly at $P < 0{\cdot}05$.

This phenotypic range is paralleled and exceeded by the tetraploids: those studied fall into two broad groups, namely, xerothermic Mediterranean types with small panicles and leaves, and strongly-lobed lemmas, score 2–3 (H, I, K, L, M, N, O), and North European with large, or very large, panicles and leaves, and almost entire lemmas, score 1–1·5 (P, Q, R, S,). Only the population from Sicily (J) is intermediate.

onThe difference in panicle size is borne out by the data in Table 4, from which it is clear the basis of spikelets per panicle that the northern diploids and tetraploids have larger heads.

Differences within populations. In order to see whether a definite relation existed within populations between the dimensions and qualities of different parts of the plant, the characters were plotted against one another in all combinations using four populations, two of subsp. *hispanica* and two of subsp. *glomerata*. For example, it might be reasonable to suppose that individuals with longer panicles would have longer basal internodes and longer glomeruli. The results showed, however, that there is no significant trend relating any pair of features from plant to plant. A similar situation has been reported for ear characters in *Lolium perenne*, which suggests that each aspect of morphology is under independent genetic control (Cooper 1960).

Heritability. The heritability of panicle length, flag-leaf length, and lemma apex morphology was studied. These characters were chosen because all are important taxonomically, and the first two might be more directly susceptible to selection pressure than the third. There was available a range of F_1 hybrids which were the result of crossing genotypes from one population of *Dactylis marina* with the following range of tetraploid forms progressively less similar in phenotype. Portugal (2), Israel (2), Scotland (1), Finland (1), Lischower (3), S. 37 (1), S. 143 (2). The depth of the lobed lemma apex was measured in millimetres; the figures in brackets show the number of crosses.

Parent/progeny regressions were calculated and compared with the correlation coefficients (Table 5). The heritability of all these characters is quite high and it is notable that the slope of the regression line is lower for panicle length, indicating that, throughout, the parents had longer panicles than the corresponding progeny. This suggests a scaling effect due to treatment and environmental differences between clonal parents and seedling progenies grown in different blocks.

Lack of correlation between characters from plant to plant within populations and high heritability suggests that all the phenotypic components studied are capable of being selected for independently. This is borne out by the F_1 data. The progeny mean values were related to mid-parent values, e.g. progenies whose mid-parent values for both panicle length and flag-leaf length were high, had high mean progeny values for both characters. However, within progeny, panicle length and flag-leaf length were not correlated from individual to individual.

Table 5. *Parent/progeny regressions and correlations. Tetraploid hybrids. Ten plants measured in each progeny*

Phenotypic character	No. of progenies	$b.yx$	Correlation coefficient
Flag-leaf length	10	0·6267	0·760
Panicle length	12	0·2608	0·829
Lemma apex	12	0·6011	0·788

All significant at $P < 0{\cdot}01$.

DISCUSSION

In any attempt to arrange the populations of the polyploid complex in a meaningful way, the adaptive radiation of, and relation between, diploids and tetraploids has to be taken into account. This discussion only applies to the genetically-balanced indigenous wild material studied, since bursts of variation may be expected when material from different areas is brought together owing to ease of hybridization.

Adaptive trends. The taxonomist places reliance on characters such as details of floral structure, which, if not directly exposed to selection, might indicate relationships not only between groups of geographical races in the tetraploid complex, but between these and the diploids as well. The data in Table 3 show many significant differences between populations in respect of lemma length, lemma apex, pubescence, and spikelet length, but only one of these, the lobed lemma apex, shows a trend when the populations are arranged on a distributional basis. This consistent variation, which also occurs in the diploids, is unrelated to the other floristic details, but correlated to the five components of panicle- and leaf-size shown in Text-fig. 2. These dimensional features are likely to be associated with the adaptive radiation of diploids and tetraploids in the colonization of a range of habitats, since it is highly probable that panicle and leaf size are directly influenced by the different selection pressures of contrasted environments.

The parent/progeny correlations show that these two features are highly heritable and therefore could be selected for independently. The fact that they are positively correlated shows that the environment influences both in the same direction.

The genetical evidence indicates that lemma apex is highly heritable and not linked to the genetic systems controlling panicle size or lemma length; the form of the lemma apex is therefore likely to vary independently of the environmental conditions unless of directly adaptive significance. If not of adaptive significance the variation trend might be indicative of relationships, in which case two primitive diploid forms could be postulated, one with lobed lemmas, the other with entire lemmas. It is not at present possible to decide to what extent lemma apex is directly susceptible to environmental conditions, and selection experiments are planned to obtain more information, from which it may be possible to assess the stability and taxonomic value of this character.

Text-fig. 2 indicates a general trend for the tetraploids to resemble the diploids in the same area. An apparent exception is Portugal. The diploid is subsp. *lusitanica*, some collections of which from north Portugal vary in the direction of *D. aschersoniana*, which resembles the northern tetraploids in many ways; the tetraploids, by contrast, are *hispanica* forms. Further study may, of course, reveal ecological reasons for this.

Taxonomy and evolution. The intra-specific classification of *Dactylis* is very difficult for the field botanist, because of the numerous geographical races. The many varieties described in the literature are of little taxonomic value. When the wider cline of variation amongst wild populations is examined we find a range from small xerothermic types to large-growing northern forms, which the inclusion of cultivated forms and their hybrid derivatives might modify and obscure.

For many botanists the classification into species and subspecies is 'experimental', depending on a knowledge of the chromosome number. As a first step, material could be divided into two groups, one with short panicles and lobed lemmas including tetraploid subsp. *hispanica* and diploids, the forms delimited by a broken line in Text-fig. 2, and another with long panicles and more or less entire lemmas including tetraploid subsp. *glomerata* and other diploids.

At present specimens cannot be determined with certainty as diploid or tetraploid solely on morphological grounds, although once the chromosome numbers are available the classification of the diploids is relatively simple, because each type is related to definite ecological conditions in a more or less restricted geographical area, and some such as *D. smithii* Link., *D. ibizensis* Gandoger and *D. juncinella* Bory, are easily identified endemics. Diploids which occur close together in Text-fig. 2, e.g. *lusitanica* and *aschersoniana*, are nevertheless complementary types differing in many quantitative, qualitative and physiological ways namely:

D. aschersoniana	*D. glomerata* subsp. *lusitanica*
Central European forests	West Portugal
Foliage 'burns' in winter	Winter green
Tall, long, nodding panicle	Less tall, shorter, stiff, erect panicle
Culm slender	Culm thick
Leaves long, slender, lax	Leaves, shorter, broader, stiff
Glabrous	Pubescent
Ligule papery	Ligule with green tissue in mid-vein

Some of the differences are apparent in Pl. 1. The genetic relation of these two taxa is under study, one object of which is to find a combination of characters which will facilitate their identification.

An ideal classification should be practical and also should reflect the evolutionary relationships of the taxa. The diploid subspecies are natural groups, well defined, and related to eco-geographical zones. At one time diploids may have been continuously distributed over wide areas. For instance Stebbins (1956) suggests that the discontinuous distribution of *D. aschersoniana* in Central Europe, the Himalayas and West China is a relict of the Tertiary period when a zone of forest stretched across Eurasia, and that *D. smithii* is also relict, since the flora of the Canary Islands where it grows contains many woody species having counterparts in Late Tertiary fossil floras.

Whether the tetraploid subspecies *hispanica* and *glomerata* are natural groups is problematical, since it is not possible to decide whether the morphological parallels between diploids and tetraploids are due (*a*) to the origin of tetraploids from diploids in the same area, or (*b*) to adaptive radiation of diploid and tetraploid into the same environments. There is, however, a third tetraploid *Dactylis marina* (Borrill, 1961) which is easily identified and is a natural group whose ancestry can be traced beyond reasonable doubt. This type, which is restricted to maritime habits in south-west Europe, the Mediterranean, and Atlantic islands, and characterized by a papillose epidermis, arose from diploids closely related to *D. smithii*, Canary Islands, and *D. ibizensis*, Balearic Islands (Borrill, 1961).

The taxonomic complexities of the genus are due to the existence of a variable tetraploid complex side by side with relict diploids, and, with the exception of *D. marina*, uncertainty regarding the relation of diploid and tetraploid forms. Although Stebbins (1956) has speculated about the evolution of the tetraploids, a great deal more information is required. Our knowledge of the diploids is incomplete, for instance, Dr Gunnar Weibull, when visiting Aberystwyth, showed me herbarium specimens of a new diploid from the Apennines. Detailed taxonomic and ecological studies are required in regions where the chromosome races are sympatric, e.g. Portugal and North Africa.

The heritability and effect of selection on what are usually regarded as reliable taxonomic characters, should be of interest to the systematist, and genetical experiments are being undertaken to assess the value of the lemma-apex in the classification of *Dactylis*.

The present paper reveals a pattern of genetic variation which may form the basis of further efforts to define morphologically what Domin calls the 'stable forms', and demonstrates the wide range of taxa, regarded variously as species or subspecies, which occur in this group.

SUMMARY

1. The main taxa of the genus *Dactylis* are surveyed, illustrating the range of species and subspecies occurring in the group.

2. The phenotypic characters in nineteen populations, including diploids and tetraploids, were analysed in detail; there were large genetic differences between the populations.

3. The within-population correlation of characters was studied and found to vary independently.

4. The heritability of some taxonomically-important morphological characters was measured, e.g. panicle length, flag-leaf length, and lemma apex. Each was highly heritable, and capable of independent response to selection.

5. The between-population correlation of morphological characters was studied. The components of panicle size, flag-leaf length, and lemma apex were related, showing a similar trend in diploids and tetraploids.

6. The significance of the trend of variation is discussed in relation to taxonomy and evolution.

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EXPLANATION OF PLATE

Tetraploid and diploid *Dactylis* species and subspecies. Representative plants grown at Aberystwyth.

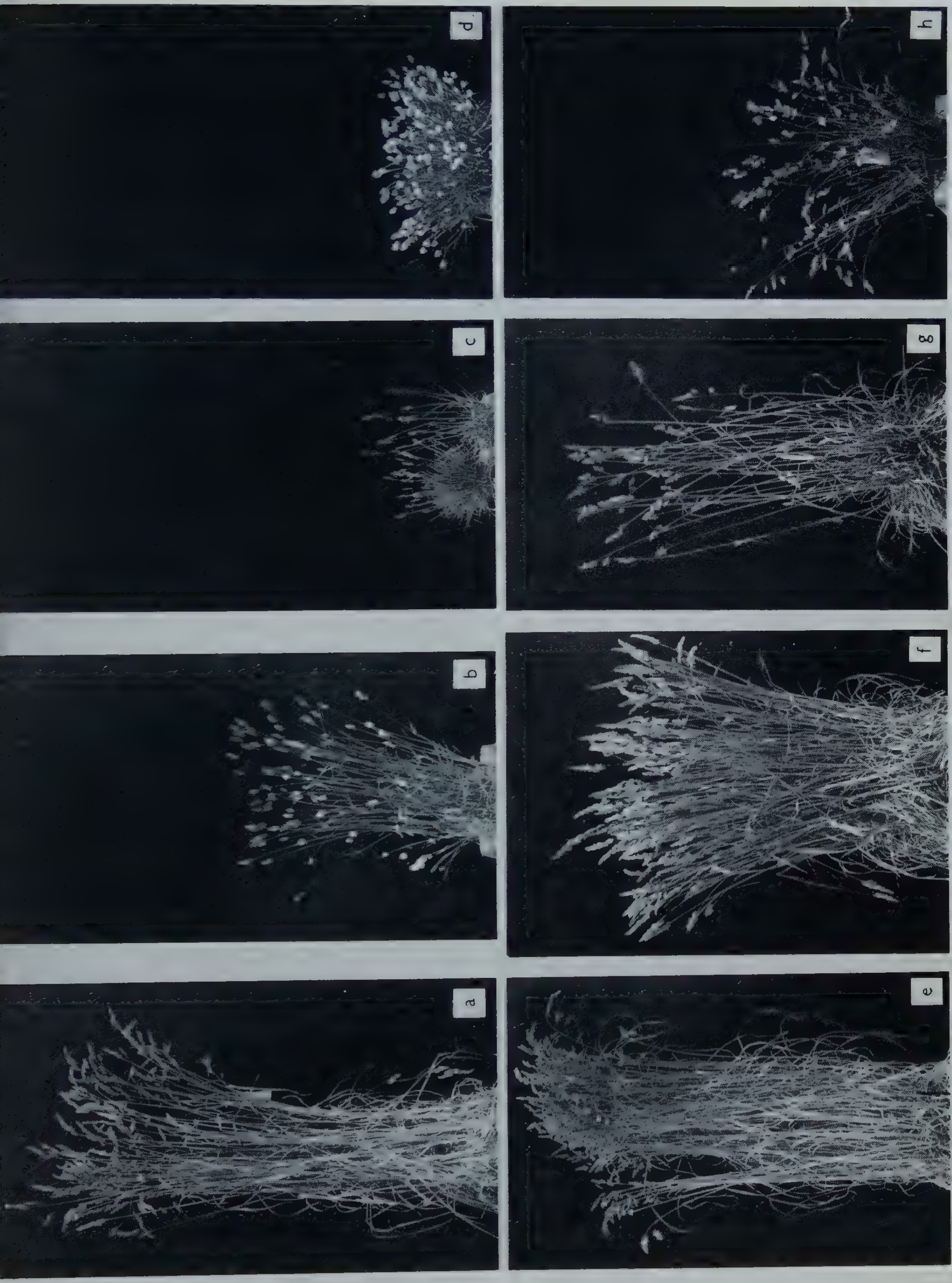
Tetraploids:

D. glomerata:

a. Subsp. *glomerata* Hayek, Denmark.
b. Subsp. *hispanica* Roth, Portugal.
c. Subsp. *hispanica* Roth, Crete. (= *Dactylis rigida* Boiss. et Heldr.).
d. *D. marina* Borrill, Portugal.

Diploids:

e. *D. aschersoniana* Graebner, Bot. Gard. Uppsala.
D. glomerata:
f. Subsp. *lusitanica* Stebbins & D. Zohary. Portuguese diploid.
g. *D. woronowii* Ovczinn. Iran.
D. glomerata:
h. Subsp. *santai* Stebbins & D. Zohary. Algerian diploid.



MARTIN BORRILL

(*Facing p.* 452)

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Epidermal characteristics in the diploid subspecies of *Dactylis glomerata* L.

BY MARTIN BORRILL, PH.D., F.L.S.
Welsh Plant Breeding Station, Aberystwyth

INTRODUCTION

It is now generally accepted that epidermal characters are of value in grass classification at all levels from the tribe to the species. This has been made abundantly clear from the classical researches of Grob (1896) and Prat (1932). More recently Church (1949) has shown that the possession of intercostal long-cells with smooth walls serves to distinguish *Glyceria* R.Br. from *Puccinellia* Parl. and *Torreyochloa* Church in which the corresponding cells have ripple walls. In addition, it is possible to distinguish between sections within these genera according to the occurrence and distribution of papillae. Borrill (1956) found that the species of *Glyceria* in Britain can be distinguished by the type of epidermis covering the leaf sheath nerves. Sørenson (1953) has shown that the epidermis provides features which are of value in identifying species of *Puccinellia*.

Recent studies in the genus *Dactylis* L. have shown that ten or more diploid subspecies occur. These are natural groups, each with a characteristic morphology, and limited geographical distribution (Borrill, 1961 *b*). The nature of the epidermis has been studied in these clearly defined forms to see whether substantial differences occur which might justify the application of the method to the whole tetraploid complex, which is difficult to classify. So far, only one natural tetraploid group *Dactylis marina* Borrill, has been recognized, in which the epidermal cells differ in shape from those of other tetraploids, and bear conspicuous papillae (Borrill, 1961 *a*).

In presenting the results, the names for the diploids proposed by Stebbins & Zohary (1959) will be used.

MATERIAL AND METHODS

Epidermal characters in the leaves were studied on living plants or herbarium material of the eight diploid subspecies shown in Table 1. Four leaves were taken from each population and these represented four genotypes except where dried material was used, when the number of plants present was not known. The leaves were not selected in any particular way except to ensure that they were fully grown and not diseased or withered. A preparation of the upper epidermis was made, using the lactic acid method described by Clarke (1960). The resulting layer of cells was usually 1 cm. long, and extended for the whole width of the leaf. Photomicrographs were made of the area halfway between the mid-vein and the leaf margin. This allowed for the gradation in cell size which occurs in this direction. Each photomicrograph included two or three inter-nerve areas, and from 50 to 250 cells, depending on the subspecies used. From this area twenty cells were selected as far as possible at random, and the following measurements were made: (1) cell length, (2) width of cell at the centre, (3) width of cell at the end, (4) stomatal length, (5) number of stomata per unit area. The data are shown in Table 1.

RESULTS: QUANTITATIVE DIFFERENCES BETWEEN SUBSPECIES

An analysis of variance revealed large and significant differences between the ten populations. For characters such as cell length and width to be of use in identifying these groups, the means obtained from repeat samples of four genotypes should fall

Table 1. *Epidermal cell data in diploid* Dactylis (see Text-fig. 1)

			Epidermal cell data			Cell shape ratios				
Subspecies	Locality	Collector	Length	Median width	Cell end width	Length / end width	Median width / end width	Guard cell length	Cell area length × median width	Stomata per unit area
a, smithii	Canary Islands	Kew Herbarium	82·9	23·48	14·66	5·6	1·61	27·7	1948	241
b, ibizensis	Balearic Islands	Prof. G. L. Stebbins (herbarium material)	176·4	22·64	14·38	12·2	1·57	30·8	3987	125
c, juncinella	Spain, Sierra Nevada	Kew Herbarium	286·6	21·58	13·73	20·8	1·57	37·0	6191	82
d, santai	Algeria, Relizane	F.A.O. (No. 3168)	212·0	26·36	18·24	11·7	1·44	36·3	5597	87
e (non-*santai*)	Algeria, Oued Chiffa	F.A.O. (No. 3215)	151·3	21·81	17·31	8·7	1·26	38·7	3298	211
f, do.	Algeria, Bouira	F.A.O. (No. 3328)	155·0	24·92	19·86	7·8	1·25	36·2	3859	142
g, judaica	Israel, Kiryat Shmuel	Prof. G. L. Stebbins, Davis, California	173·4	29·51	19·53	8·8	1·50	42·8	5115	130
			204·8	29·32	19·77	10·8	1·47	41·4	6001	—
h, woronowii	Iran, Arak	F.A.O. (No. 3697)	252·0	30·85	18·84	10·8	1·63	46·9	7762	83
j, lusitanica	Portugal, Sintra	Prof. A. Camara, Estaçao Agronomica Naçional, Sacavem	237·2	25·61	17·03	13·9	1·50	33·0	6072	82
			213·6	23·80	17·08	12·4	1·39	36·7	5084	—
k, aschersoniana	—	Botanic Garden, Uppsala	212·6	23·34	17·91	11·8	1·30	32·0	4954	108
			204·3	25·15	18·19	11·2	1·37	31·9	5148	—
	Significant differences $P < 0·01$		30·8	0·25	0·19	—	—	0·21	—	—

(Analysis of variance on 10 populations, 4 genotypes, 20 cells from each; linear dimensions in μ.)

within the range of variation permissible at $P < 0{\cdot}01$. Measurements were therefore made on a further four plants of subspecies *judaica*, *g*; *lusitanica*, *j*; and *aschersoniana*, *k*.

Those of *judaica* were from the same population, and this applies also to *aschersoniana*, because the plants were derived from a further batch of seed obtained from the same mother plants in the Botanic Garden, Uppsala. The repeat sample of *lusitanica*, however, originated from a different wild population.

Table 1 shows to what extent the figures for the duplicate samples agree with the original means. The most consistent values are shown by the means for cell length, and width of the cell end, which do not differ significantly from the original observations, whether the duplicates derive from the same population or not. The repeat data for median width and guard cell length suggest that these characters would be less reliable as a means of identification.

In Text-fig. 1 the sample means are plotted, using cell length and width as ordinates. There is no correlation between these characters from population to population, although the data show a very close relation between the length and width of individual cells within each group. The rectangles surrounding the means show the limit of variation at $P = 0{\cdot}01$. Although two pairs of groups overlap, *d* and *k*, *g* and *f*, the others can be separated using these characters. Similarly, Martin (1954), using cell length and width in leaf cuticles, found it possible to distinguish between certain species, including grasses such as *Festuca pratensis* Huds. and *F. rubra* L.

Stomatal length appears to vary independently, since no correlation has been found with stomatal frequency, cell length, or any of the other features studied either within or between groups.

The number of stomata per unit area varies considerably, and scatter diagrams were prepared to test the relation between frequency, and cell length, cell size (area), and cell shape, both within and between populations. A highly significant negative correlation with a coefficient of $-0{\cdot}945$ was obtained between populations for stomatal frequency and cell length. It seems probable that other factors, such as the number of veins, will also influence this frequency, since in many cases the stomata are arranged in rows closely associated with the nerves.

Variations in cell shape can be assessed quantitatively in two ways, by finding the ratios length:end width and median width:end width. The former is a reliable composite character in identification. The latter, while giving a quantitative assessment of the range from square to hexagonal cells in the populations, is not so satisfactory, due to the variation in median width encountered between duplicate samples.

RESULTS: QUALITATIVE DIFFERENCES BETWEEN SUBSPECIES

In addition to the differences shown by the numerical data, there are others, mainly qualitative in character, which are of value in separating the diploid *Dactylis* groups. These are (Pl. 1 and Text-fig. 1):

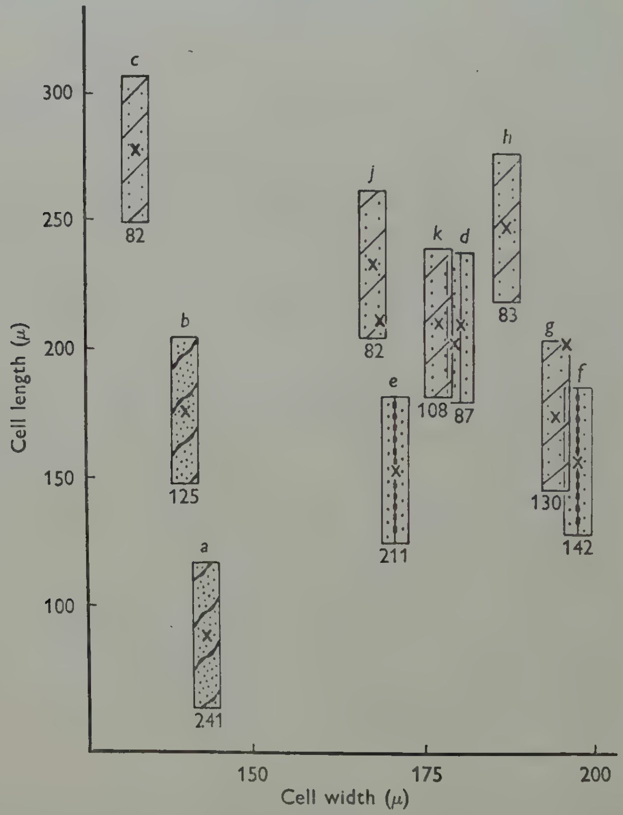
(1) There is a wide range in cell shape of which two aspects have been studied. The first is the degree to which the cells are hexagonal or square. This is measured by the ratio width at centre of cell:width of cell end. Amongst the populations, *a*, subspecies *smithii*, has markedly hexagonal cells, and at the other extreme are the populations *d*, *e*, and *f*, from Algeria with square cells. The second aspect of cell shape is measured by the ratio length:width of cell end. In this respect the most extreme forms are subspecies *juncinella* in which the cells are 20 times as long as wide, and subspecies *smithii* in which length exceeds width by only 5 times.

(2) The anticlinal cell walls can be classified as three main types, which are sinuous, beaded, or smooth, respectively. In the subspecies *smithii* and *ibizensis*, the walls are sinuous in varying degree, this being most pronounced in *smithii* (Borrill, 1961*a*). Two

of the Algerian populations, *e* and *f*, have beaded cell walls; this shows most clearly in *e*, (Pl. 1). The remainder have smooth walls.

(3) The distribution of the stomata which lie in rows flanking the nerves, except in subspecies *smithii* and *ibizensis* where they are more uniformly distributed.

All these features of the groups are illustrated in Text-fig. 1. From the point of view of identification, the most difficult pairs are first, Algerian *d* and *aschersoniana k*, and secondly, Algerian *f* and *judaica g*, which have similar cell dimensions. The first pair can be separated by cell shape, cubical in *d*, hexagonal in *k*, and the second pair by the type of cell wall, beaded in *f*, smooth in *g*, and, to a lesser extent, by cell shape and stomatal frequency.



Text-fig. 1. Epidermal cell characteristics of diploid *Dactylis* subspecies (data in Table 1). *Key*: *a*, *smithii*; *b*, *ibizensis*; *c*, *juncinella*; *d*, Algerian subsp. *santai*; *e* (non-*santai*); *f*, Algerian (non-*santai*); *g*, *judaica*; *h*, *woronowii*; *j*, *lusitanica*; *k*, *aschersoniana*.

cells hexagonal //
cells cubical ||
cell walls: smooth /
sinuous /
beaded /
stomata: scattered ⁘
in rows along nerves ⁞⁞

The figures indicate the number of stomata per unit area.

In the group with more or less hexagonal cells, the subspecies *smithii* and *ibizensis* have sinuous cell walls and uniformly distributed stomata. Subspecies *juncinella* has very long slender cells. Populations *g*, *h*, *j* and *k* which complete this group can be separated by cell width, and *g*:*h* (subspecies *woronowii*:*judaica*), and *g*:*j* (subspecies *woronowii*: *lusitanica*) by cell length as well.

The data reveal some diversity amongst the populations from Algeria all of which have more or less square cells; *d* has smooth-walled, rather long cells, and a low stomatal frequency, whereas *e* and *f* have cells with beaded walls. These latter two groups differ markedly, *e* having much narrower cells and higher stomatal frequency than *f*.

DISCUSSION

The results of this epidermal survey show that the method of sampling employed has proved capable of distinguishing between the taxa, particularly in regard to cell size. The cells were selected from a constant position on the leaf, thus taking into account the gradation in size which occurs from mid-vein to margin, and to a lesser extent from ligule to leaf-tip (Soper & Mitchell, 1956); but cell size, notably length, can also vary according to the position of the leaf on the shoot (Borrill, 1959). Greater precision in sampling could therefore be obtained if a particular leaf, say number 6, was selected on the main shoot of seedlings grown together in the same environment.

Such a method might be useful to detect small differences in epidermal pattern between populations in taxonomic groups such as subspecies. It is now being applied to herbage strains to assess the order of difference found among tetraploid populations.

In the group of populations which make up the diploid *Dactylis* subspecies, natural selection appears to have led to physiological and genetical adaptation to diverse, and sometimes extreme, environments. The resulting large differences in epidermal phenotype must in part represent functional integration in relation to these environments.

Amongst the cell characters studied the following are of value in grouping populations: (1) The extent to which the cell wall is smooth, sinuous, or beaded; (2) the type of stomatal distribution; (3) the extent to which the cells are hexagonal or square. This suggests that these characters may have been more stable during the evolution of the taxa, because less subject to environmental selection. With regard to the third character, there is clear evidence from Cretan tetraploids (Borrill, unpublished) that although the ratio cell length: cell end width shows a cline of variation in relation to altitude, all the populations have cells which are hexagonal to a similar degree.

When the subspecies are placed in groups based on these characters the arrangement conforms with their geographical distribution.

Subspecies *smithii* and *ibizensis* possess uniformly distributed stomata, and the walls of the longitudinal cell rows are more or less sinuous. Both are endemic in the Canary and Balearic Islands respectively. Detailed studies have shown that the form of these cells is related to the production of epidermal papillae. This is exemplified by the related tetraploid *Dactylis marina* and its hybrids, in which the form of the cells can range from long, hexagonal, as is usual in *Dactylis*, through shorter, intermediate types with bulging sinuous longitudinal cell walls, to cells bearing a large spherical papilla. This character is under polygenic control. In both these diploid subspecies the cells are mainly of the intermediate type, although in subspecies *smithii* the genetic background is such that in a few of the cells the wall bulges sufficiently to form a papilla (Borrill, 1961 *a*).

The populations from Algeria, distinguished by more or less square cells, are heterogeneous in their gross morphology, and *d* appears to fall within the limits of subspecies *santai* (Stebbins & Zohary, 1959). The others, *e* and *f*, characterized by beaded cell walls, are phenotypically rather similar (Borrill, 1961 *b*), but differ in cell size. In *f* the beading of the cell walls is less pronounced and the general form of the epidermis shows some similarity with subspecies *judaica* or *woronowii*. Both *e* and *f* originated in a cultivated area with arable cropping, and it is possible that man's activities have provided opportunities for hybridization between the groups of diploids in this region.

Further sampling of the diploids in North Africa is required in order to clarify their taxonomic status.

The remaining group of subspecies *judaica* and *woronowii*, *lusitanica*, *juncinella* and *aschersoniana* possess hexagonal cells. Subspecies *juncinella*, endemic at high altitudes in the Sierra Nevada in Spain, is a somewhat isolated form, with a distinctive pattern of very long epidermal cells. All these types can be separated from one another by differences in epidermal cell size.

These observations on *Dactylis* add to the growing body of evidence indicating the value of epidermal studies in plant classification. There is reason to suppose that quantitative studies of cell size will be very useful in this field when considered in relation to the qualitative characters on which the main emphasis has hitherto been placed.

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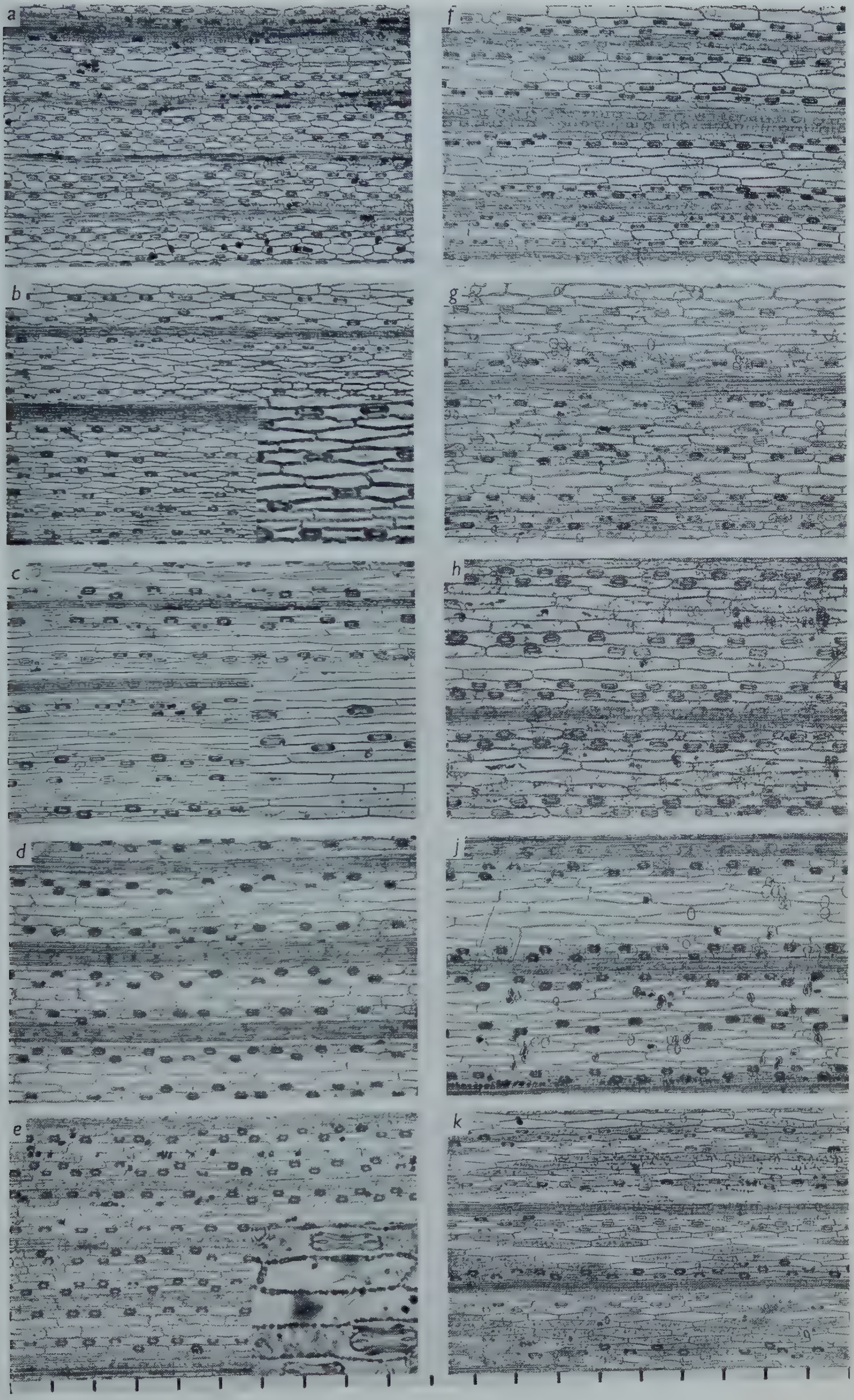
EXPLANATION OF PLATE

PLATE 1

The upper leaf epidermis of diploid *Dactylis* subspecies. *a*, *smithii*; *b*, *ibizensis*; *c*, *juncinella*; *d*, Algerian (subsp. *santai*); *e*, Algerian (non-*santai*); *f*, Algerian (non-*santai*); *g*, *judaica*; *h*, *woronowii*; *j*, *lusitanica*; *k*, *aschersoniana*. 1 division = 100μ. Enlargements 1 division = 50μ.



MARTIN BORRILL

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The taxonomy and nomenclature of certain palmelloid, planktonic, green algae described previously

By J. W. G. LUND, F.L.S.

Freshwater Biological Association, Ambleside, Westmorland

Since the description (Lund, 1956) of certain planktonic algae I have received, through the kindness of Professors A. M. Matvienko of Kharkov and J. V. Roll of Kiev, an article and a book by Korshikov (1941, 1953) which were unknown to me. In these Korshikov describes and figures most of them under different names. In addition, Bourrelly (1959) and Ettl (Komarek & Ettl, 1958) have considered *Gemellicystis* Teiling and *Cecidochloris* Skuja. The following is a revision of the nomenclature and taxonomy of these algae in relation to these works and some additional observations.

(1) *Coenococcus planctonicus* Korshikov, 1953 (*Radiococcus planktonicus* Lund, 1956: 594)

Although I have often seen this alga in the plankton of Windermere in the last four years and used clonal cultures for experimental purposes no features additional to those already described have been detected.

In placing this alga in *Radiococcus*, I followed Teiling (1946) in not considering the fine, radially striated mucilage of the envelope a character of generic importance, although it is present in the species previously described. Korshikov (1953) describes a number of azoosporic algae which form microscopic, mucilaginous colonies which only differ in the shape and arrangement of the cells within. For these he erects three new genera, *Coenocystis*, *Coenochloris* and *Coenococcus*, which lie near to *Sphaerocystis* Chodat *pro parte* and *Radiococcus* Schmidle.

Coenochloris differs from *Coenococcus* in the grouping of the cells (autospores) closely together in the centre of the colony. In *Coenococcus* they are dispersed more or less irregularly and the centre of the colony is often free of them (Korshikov, 1953, figs. 295, 296*a*, *Radiococcus planktonicus* Lund, 1956, fig. 1A, C). From *Radiococcus* both genera differ in the absence of radially striated mucilage. The cells of young colonies of *Coenochloris* (e.g. Korshikov, 1953, fig. 296*b*, 297*a*) are in the very centre of the colony, but this feature is less marked in older colonies. *Coenocystis* also has structureless mucilage, the cells are elongate and not restricted to the central area of the colony.

The position of *Sphaerocystis* is not clarified by Korshikov. He never saw zoospores (cf. Lund, 1952) and agrees that it has nothing to do with *Gloeococcus* Braun (Lund, 1952, 1957). He does not figure it, in marked contrast to almost every other species in his magnificent monograph. It seems, then, that although he says it is a common alga he has not studied it in detail. This does not resolve the problem as to what are the limits of this residue of Chodat's (1897) genus. *S. schroeteri* would appear to come close to *Coenococcus*. *S. polycocca* of Korshikov (1953: 327, fig. 301) is so different that it should be placed in another genus. It resembles some of the stages of *Gloeocystis planctonica* (Naeg.) Lemm. in Skuja (1948, Taf. XII, figs. 2, 4).

In these genera there are some differences in the fate of the wall of the mother cell during reproduction, but it is not clear that these are significant taxonomically.

Korshikov says that the cells of *Coenococcus planktonicus* are liberated by the mucilaginization of the wall of the mother cell, this being the only respect in which his account of *Coenococcus planktonicus* differs from mine of *Radiococcus planktonicus*. In my material however, pieces of this wall may sometimes be seen faintly after liberation of the autospores (Lund, 1956, one such piece shown in fig. 1 C). Therefore this does not seem to be a real point of difference on which a separation might be based.

It may be questioned whether the differences between *Radiococcus*, *Coenococcus*, *Coenocystis* and *Coenochloris* are of generic value. (I exclude *Sphaerocystis* from this consideration since the identity of its type species, *S. schroeteri*, is too uncertain for the name to be used). However, it is impossible to answer this question for we know nothing of the cytogenetics of these algae. The distinctions are in accord with present practice in the Chlorococcales where a large part of the taxonomy is based on convenience for identification. The retention of these genera also avoids changes in nomenclature which are no more likely to be final than the present arrangement.

Since their cells are not centrally located in a wide, radially striated mucilage investment, *Radiococcus planktonicus* Lund and *R. pelagica* Teil, are therefore best removed from that genus and placed in *Coenococcus*. The correct name for the first is then *C. planctonicus* Korsh. and for the second *C. pelagicus* (Teiling) comb.nov. (*Radiococcus pelagicus* Teiling, 1946).

(2) *Cecidochloris adnata* (Korsh.) comb.nov. (*Chlorophysema adnata* Korshikov, 1941; *Cecidochloris stichogloeae* Skuja, 1948: 100; see also Lund, 1956: 595)

Skuja and I were unaware that this alga had been described previously as *Chlorophysema adnata* Korshikov (1941: 62).

Skuja (1948) found that a characteristic feature was the solution of the mucilage of the host colony, *Stichogloea doederleinii* (Schmidle) Wille. He also found the species occasionally on other mucilaginous, colonial algae, but it is not clear whether he saw the same solution of the mucilage in these hosts. Korshikov (1941) and I (Lund, 1956) did not observe this; indeed we both observed it on algae which do not have mucilage sheaths (*Asterionella* and *Dinobryon*). It does not seem absolutely certain that what Skuja observed was the destruction of the mucilage of the host. When immersed in *Staurastrum anatinum* Cooke & Wills (Lund, 1956, fig. 1 D, F, G, H) there is no sign of this. The alga is completely surrounded by the mucilage of the host plant. Skuja (1948) says that it leaves a clear pock mark. If, however, the developing *Cecidochloris* pushes aside the surface mucilage of the host during the enlargement of its membrane, the result may look the same. The hole left by it will fill up if the mucilage of the host alga is diffluent enough to flow back or if new mucilage is produced.

Equally, if Skuja's interpretation is correct, this solution of the host mucilage does not seem to be a generic difference judging from his own accounts of *Chlorophysema microcystidis* Skuja (1956: 156–7, Taf. 22, figs. 31–33, Taf. 23, figs. 1, 2), an alga which Ettl (1958) transfers to *Chlorangium* because the cells do not lie in the inflated vesicle developed from the wall of the mother cell. Skuja only distinguishes *Cecidochloris* from this species by the absence of a basal stalk (foot), the ability of the vegetative cells to become motile, and the insertion of the daughter colonies within the enlarged membrane of the mother cell (Einschachtelung). Whether the stalk of *Chlorophysema microcystidis* becomes immersed in the host by dissolution of its mucilage is not stated.

The direct metamorphosis of vegetative cells into swarmers is really only the normal formation of zoospores with the development of motility delayed while growth continues. This is the difference between volvocine and chlorococcoid (incl. palmelloid and dendroid forms) green algae. In zoosporic coccoid forms assumption of motility is not possible after the daughter cells have reached a certain stage in development, and hence only zoospores can be produced. The reason why there is no clear demarcation between these groups of motile and non-motile algae is that this 'certain stage' may be reached early or late so that there are all transitions between a phase of motility and one without motility. This may be seen in a series of species and genera, or in one and the same species (e.g. palmelloid stages of terrestrial species of *Chlamydomonas* and species of *Chlorococcum*).

Can the genus *Cecidochloris* Skuja (1948) be separated from *Chlorophysema*? The latter was erected (Pascher, 1927) to include species of *Chlamydomonas* in whose life-history the non-motile phase is dominant. These algae (see also Pascher, 1940) are attached to various substrata by a pad or stalk, which may be only a low cushion of iron-encrusted material. They differ from allied genera (see Ettl, 1958) in the enlargement of the membrane so that the original cell and the following generations (usually one or two) lie in an inflated vesicle, a condition only found in some of the other genera during the development of the zoospores (e.g. Pascher, 1927, fig. 440*d*, *g*: *Chlorangium inhaerens* (Bachm) Ettl, 1958).

Ettl (1958) places Anachin's (1929–30) *Chlorophysema sessilis* in *Cecidochloris* since the habit and cell structure are identical. Pascher (1940) had previously said that this species does not belong to *Chlorophysema* but gave no reasons; Korshikov (1953) retains it in this genus. However, Ettl (1958: 333) says *Chlorophysema* and *Cecidochloris* have the same cell structure, the latter being characterized by its habit, that is living in the mucilage of other algae. This ignores the fact that *Cecidochloris stichogloeae* Skuja (*Chlorophysema adnata* Korsh.) lives also on algae without mucilage (Korshikov, 1941, 1953; Lund, 1956). There does not seem to be any distinction on Ettl's grounds.

The only possible distinction seems to be the formation of some kind of attachment organ in *Chlorophysema*. A stalk is formed in *C. inertis* (Korsh.) Pasch., *C. apiocystiforme* (Artari) Pasch., *C. contractum* Pasch. and *C. ampliata* Skuja. Transitions to a ferruginous pad or solely this are seen in *C. inertis* p.p., *C. ellipsoideum* Pasch., and *C. ovalis* Skuja. Figures and details of these species may be found in Pascher (1927, 1940), Korshikov (1953), Skuja (1956), and Ettl (1958). Korshikov (1953) says on p. 70 that the cells are attached to the substratum by a beak, but in his key on p. 71 separates *C. sessilis* and *C. adnata* from the other species by the absence of a beak.

As *Chlorophysema sessilis* Anachin and *C. adnata* Korsh. agree in the absence of any definite attaching organ or basal iron incrustation they are best transferred to *Cecidochloris* as *C. sessilis* (Anachin) Ettl and *C. adnata* (Korsh.) comb.nov. (*C. stichogloeae* Skuja), with the change that the grounds for generic separation are not those of Ettl (1958) or Skuja (1956), but this absence of an attaching organ. This is in agreement with the taxonomic importance generally placed on the presence or absence of this feature in the Chlorococcales and Chlorangiales. It also avoids further changes in nomenclature.

(3) *Gemellicystis imperfecta* (Korsh.) comb.nov. (*Tetraspora imperfecta* Korshikov, 1941: 60; *Gemellicystis neglecta* Teiling, 1946: 67, emend. Skuja, 1948: 110; see also Lund, 1956: 598, Bourrelly 1959: 40, incl. *G. lundii* Bourrelly, 1959).

All the accounts cited above are more or less at variance with one another. The essential generic features on which there is now agreement are as follows: the cells are arranged in pairs, apex to apex. When young they are apically flattened, but before the next division are generally globose. These pairs are further arranged in loose, irregular groups of four or more cells dispersed within a wide mucilage envelope which may itself split into two parts. The massive, basically cup-shaped, chromatophore contains a large basal pyrenoid. Two anterior contractile vacuoles are present.

The points of disagreement are the presence or absence of pseudocilia and flagella, a stigma in the non-motile stage, and the detailed structure of the chromatophore and the starch sheath to the pyrenoid. In addition to these accounts, algae showing certain strong resemblances to *G. neglecta* have been described by Woronichin (1931) and Korshikov (1941) as *Pseudosphaerocystis planctonica* Woronich. and *Tetraspora imperfecta* Korsh.

Teiling (1946) depicted as pseudocilia short threads which are undoubtedly two flagella (Skuja, 1948; Lund, 1956), a feature which I have checked on several occasions in the last two years. Pseudocilia were believed to be absent (Skuja, 1948; Lund, 1956), though curious interrupted thread-like structures were visible in colonies stained in Lugol's solution (Lund, 1956, fig. 3G). These were thought to be artifacts, but I have since observed them with the aid of cotton blue and under phase contrast. They are not always detectable, but when present there are never more than two to each cell. They arise from the front end and almost at once bend backwards sharply. They may reach the periphery of the mucilage, but I have never seen them outside it.

The reason why Teiling (1946) did not see contractile vacuoles or a stigma seems to be that he examined preserved material. Thus in his figure 2 the mucilage envelope is strongly contracted as is normal when formalin or other fixatives and stains are added.

The British specimens were said to have a stigma (Lund, 1956) and its occasional apparent absence could have been an oversight because of its minute size. Skuja (1948) found that the Swedish ones did not have a stigma but this did appear when vegetative cells assumed motility. Bourrelly (1959) says a stigma is often present. Further examination has shown that these accounts are not as divergent as originally appeared. A stigma is not always present in the vegetative cells, but in the British specimens very commonly is (cf. Bourrelly, 1959). Skuja (1948) is therefore wrong in denying its presence but is probably right in relating the development of a stigma to the assumption, or potential assumption, of motility. A stigma is, however, often present in non-motile cells lacking flagella.

Bourrelly (1959) has divided the *G. neglecta* of the authors into two species. *G. lundii* has an undissected chromatophore unlike that described by Skuja (1948). The starch sheath to the pyrenoid consists of two caps, one lining the anterior and the other the posterior part of the pyrenoid, with a small gap between them. It is perhaps significant that he says that this gap is 'signe probable de croissance', if by this he refers to cell development. *G. neglecta* Teil. has an apically dissected chromatophore (Skuja, 1948, Taf. XI, figs. 14, 16–21) and has, according to Skuja, a granular starch sheath to the pyrenoid. Whether Bourrelly is correct in applying this name to Skuja's description seems uncertain. The type description (Teiling, 1946: 67) mentions neither of these features. Bourrelly (1959) presumably considers that as both Teiling and Skuja found it commonly in Sweden they must have been observing the same alga. But Bourrelly (1959) and Lund (1956) failed to find the characteristic chromatophore and Teiling recorded his alga from Italy and Germany. It seems unlikely that only one species exists in Sweden and another in various parts of Europe (see also Jaag & Nipkow (1951)). Dr H. M. Canter has also found specimens in formalin material from Finland which agree with Teiling's (1946) description of *G. neglecta*. However, further examination of British material, from the same lakes as before, leads to the view that both these algae belong to the same species which can therefore be called *G. neglecta* Teil. em. Skuja (syn. *G. lundii* Bourr.). Sometimes in British specimens the chromatophore is not unbroken, though I have never seen such dissected specimens as some of those depicted by Skuja. Indeed it appears that not all the Swedish specimens have dissected chromatophores (e.g. Skuja, 1948, Taf. XI, fig. 15), while it seems that this feature may easily be overlooked (cf. Skuja's drawings at lower magnification, 1948, Taf. XI, figs. 10–13). Skuja says 'von aussen ± median zerschlitzt' and 'interdum extus longitudinalites irregularitusve striato' (Skuja, 1948: 112, 111). In British material, when the cells are observed from above, the upper margin of the chromatophore may sometimes be seen to be somewhat undulate, and from the side to have one or two slits. These features are easily overlooked because the chromatophore is so massive that the undulations or slits are masked by the parts beneath, only becoming visible by careful focusing with an immersion lens.

Pseudosphaerocystis planctonica Woronichin (1931) (see Korshikov, 1953: 74) is so like *Gemellicystis neglecta* that despite the sketchy description the only significant difference seems to be the occasional presence of a papilla (compare the two cells in fig. 17*b*, Korshikov, 1953). This papilla has not been seen in the rich material examined by myself or Skuja (1948) and so *Pseudosphaerocystis planctonica* cannot be considered as synonymous with *Gemellicystis neglecta*. On the other hand, it seems certain that it does belong to the latter genus and is, therefore, better named *Gemellicystis planctonica* (Woronichin) comb.nov.

Tetraspora imperfecta Korshikov (1941: 60) is also so like *G. neglecta* that the only question concerning its identity with it is over the pseudocilia. The apparent absence of a stigma, flagella or dissected chromatophores is clearly not significant from what has been said already. Korshikov's statement concerning the pseudocilia is in translation as follows:

> As regards the pseudocilia, in the vast majority of cases they are completely absent. Only by very careful investigation, with the help of immersion objectives, can one sometimes see on the anterior end of the cells faintly visible mucilaginous lumps or threads, which form probably because of the destruction of the pseudocilia in the very beginning of their formation. In certain cases I was able to see on the front end of the cell pairs of tiny mucilaginous globules, resembling those which get formed from the aggregation of threads (fig. 3). Thus in fact the pseudocilia are here as if reduced and this was the cause of my naming the organism *T. imperfecta*. However, careful examination of a large number of colonies showed that in some cases the cells have a supply of real pseudocilia and this permits me to include the given organism in the genus *Tetraspora*, despite a series of peculiarities unusual for this genus. In figure 4 two cells with pseudocilia are depicted. The latter were so thin that only with immersion lenses and strained attention did I succeed in tracing them from the beginning to the end and in depicting them with the help of a drawing apparatus. The contour of the mucilage is invisible by normal investigation and was drawn after application of indian ink. The length of the pseudocilia was about 60μ. Immediately from their base they bend in the opposite direction backwards to the periphery, coming forward out of the mucilage into the surrounding water for approximately half their length. They stain with extraordinary difficulty and this greatly impedes their being found. In material from the river Niva the cells apparently always had pseudocilia.

In order to ensure, so far as possible, that Korshikov's exact meaning is not altered, I have translated this passage in a literal manner.

Korshikov's and my observations agree in several respects. The pseudocilia are always difficult to see. This may or may not mean that he is correct in saying that they are often really absent. When seen their course is very difficult to follow. They bend backwards in a very characteristic manner. His observations differ from mine in the occasional presence of mucilaginous bubbles in the place where at other times pseudocilia are found and the passage of pseudocilia well beyond the mucilage investment. The 'bubbles' may be of different character or related to the production of flagella. That the pseudocilia did indeed project beyond the edge of the colony and were not extruded during contraction of the mucilage in stains or fixatives is clear from Korshikov's use of indian ink. Korshikov (1941, Tab. 3, fig. 4) shows them as continuous lines in contrast to my broken lines (Lund, 1956, fig. 3G) but this is probably because I have drawn the parts of the protoplasm which stain and are not continuous in pseudocilia. It is just such parts which are likely to be stained by iodine and cotton blue and to stand out in phase contrast.

There can then be no doubt that at least part of the material included in *Tetraspora imperfecta* is identical with *Gemellicystis neglecta*. The only uncertain part of Korshikov's (1953) material is that found in the River Niva in which all the cells had pseudocilia. *Tetraspora imperfecta* Korsh. may therefore be typified by the organism on which the major part of his description is based and the Niva material excluded as being either aberrant or belonging to a different organism. Then *T. imperfecta* Korsh. as typified here has priority over Teiling's (1946) *Gemellicystis neglecta*. The alga should be separated from *Tetraspora* because of the characteristic cell arrangement and structure, while even if the pseudocilia really are such, they are indeed imperfect and unlike those of *Tetraspora*. The name should then be *Gemellicystis imperfecta* (Korsh.) comb.nov.

(4) *Paulschulzia pseudovolvox* (Schulz) Skuja, 1948: 118 (*Tetraspora pseudovolvox* Schulz, 1923; *T. simplex* Korshikov, 1941; *Schulziella pseudovolvox* Teiling, 1942)

The range of structure described and depicted for *Tetraspora simplex* Korshikov (1941) is within that in Schulz (1923), Teiling (1942), Skuja (1948) and Lund (1956). Skuja's name has priority as it is based on *T. pseudovolvox* Schulz (1923, *Schulziella pseudovolvox* Teil.). The genus is clearly distinct from *Tetraspora* (Lund, 1956).

(5) *Paulschulzia tenera* (Korsh.) comb.nov. (*Tetraspora tenera* Korshikov, 1941; *Tetraspora elegans* Woronichin, 1949; *Paulschulzia elegans* (Woron.) Fott, 1954; *P. elegans* (Woronich.) Lund, 1956)

Tetraspora tenera Korshikov (1941) is identical with *P. elegans*. Since this name has priority over Woronichin's (1949) *Tetraspora elegans*, the correct name is *Paulschulzia tenera* (Korsh.) comb.nov.

The author's thanks are due to Mr R. Ross for kindly criticizing the manuscript and especially for advice on nomenclature, and to his wife (Dr H. M. Canter) for checking the observations on the chromatophores of *Gemellicystis neglecta*.

SUMMARY

On the basis of further investigation and literature previously unobtainable, the correct names and synonymy of certain palmelloid planktonic green algae is considered to be as follows:

(1) *Coenococcus planctonicus* Korsh. (*Radiococcus planctonicus* Lund.).
(2) *Coenococcus pelagicus* (Teil.) comb.nov. (*Radiococcus pelagica* Teil.).
(3) *Cecidochloris adnata* (Korsh.) comb.nov. (*Chlorophysema adnata* Korsh.; *Cecidochloris stichogloeae* Skuja).
(4) *Gemellicystis neglecta* Teil. non Bourr. (*Tetraspora imperfecta* Korsh.; *Gemellicystis neglecta* Teil. sensu Bourrelly (1959); *G. lundii* Bourr.).
(5) *Gemellicystis planctonica* (Woronich.) comb.nov. (*Pseudosphaerocystis planctonica* Woronich.).
(6) *Paulschulzia pseudovolvox* (Schulz) Skuja (*Tetraspora pseudovolvox* Schulz.; *T. simplex* Korsh.; *Schulziella pseudovolvox* Teil.; *Paulschulzia pseudovolvox* (Schulz em. Teiling)).
(7) *Paulschulzia tenera* (Korsh.) comb.nov. (*Tetraspora tenera* Korsh.; *T. elegans* Woronich.; *Paulschulzia elegans* (Woronich.) Fott; *P. elegans* (Woronich.) Lund.).

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The anatomy of *Canna*

By P. B. TOMLINSON*

Communicated by the Botanical Secretary

INTRODUCTION

In two recent articles in the present series dealing with the vegetative anatomy of the Scitamineae the anatomy of the Zingiberaceae (Tomlinson, 1956) and Musaceae (Tomlinson, 1959) has been outlined. The present paper describes the anatomy of the Cannaceae in the same way. It is hoped to complete an account of the anatomy of the Marantaceae in the near future, whereupon it should be possible to draw some general conclusions about the systematic implications of anatomical evidence for the classification of the whole of the Scitamineae.

The anatomy of the Cannaceae has been described previously by Solereder & Meyer (1930). My own account is based on this earlier summary, supplemented by observations on fresh material of *C. coccinea*, *C. indica*, *C. orientalis* and an unnamed *Canna* hybrid, all cultivated at Achimota. The techniques employed in fixing and sectioning this material were the same as those applied to the Zingiberaceae and Musaceae and described fully in the two previous papers.

GENERAL MORPHOLOGY

Canna is the sole member of the family Cannaceae and includes about fifty species. Their nomenclature seems to be very confused and many hybrids of unknown origin exist. Although the original home of *Canna* is the American tropics, species are now widely distributed throughout tropical regions both as garden ornamentals and attractive, but scarcely pernicious, weeds. Even though *Canna* is a tropical genus many species are half-hardy in quite high latitudes and the more showy hybrids are common as bedding plants in temperate regions. Queensland Arrowroot is the starch extracted from the rhizome of *Canna edulis* and *C. indica*.

In its vegetative morphology (and anatomy) *Canna* is very uniform. It has a sympodially-branched rhizome with long fleshy segments which bear distichously arranged scale-leaves separated by distinct internodes. Each rhizome segment ends in an erect leafy shoot bearing a terminal inflorescence. At the base of each erect shoot there is a brief transition from scale-leaves to foliage leaves but there is no transition from foliage leaves to bracts. The foliage leaves are inserted distichously, each node being marked by a slight swelling. The leaves allow *Canna* to be readily distinguished from most other members of the Scitamineae. Each leaf has an open, encircling leaf sheath (not closed as in *Costus*), eligulate and passing gradually (not abruptly as in *Heliconia* or ligulate as in the Zingiberaceae) into an indistinct petiole (not pulvinate as in the Marantaceae) which becomes the midrib of the ovate-lanceolate lamina. The veins of the lamina have a more or less sigmoid course, passing acutely from the midrib region and approaching the entire leaf margin almost asymptotically. In the middle part of their course the veins are parallel with each other and connected by weak transverse commissures. Of the other members of the Scitamineae, *Orchidantha* (Lowiaceae) most resembles *Canna* in its leaf morphology.

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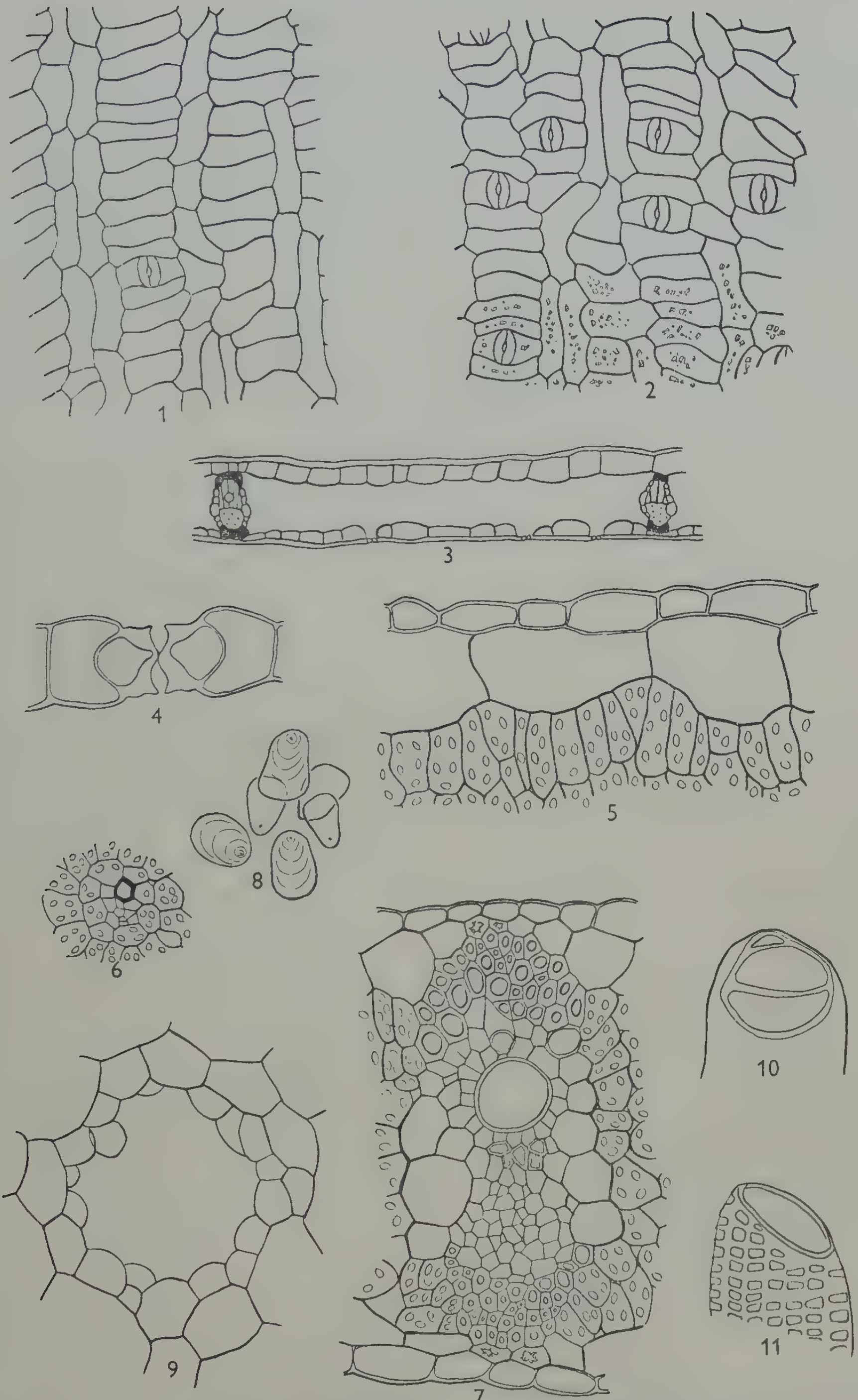
* This work was carried out whilst the author was on the staff of the Department of Botany, University College of Ghana, Achimota, Accra.

GENERAL ANATOMY

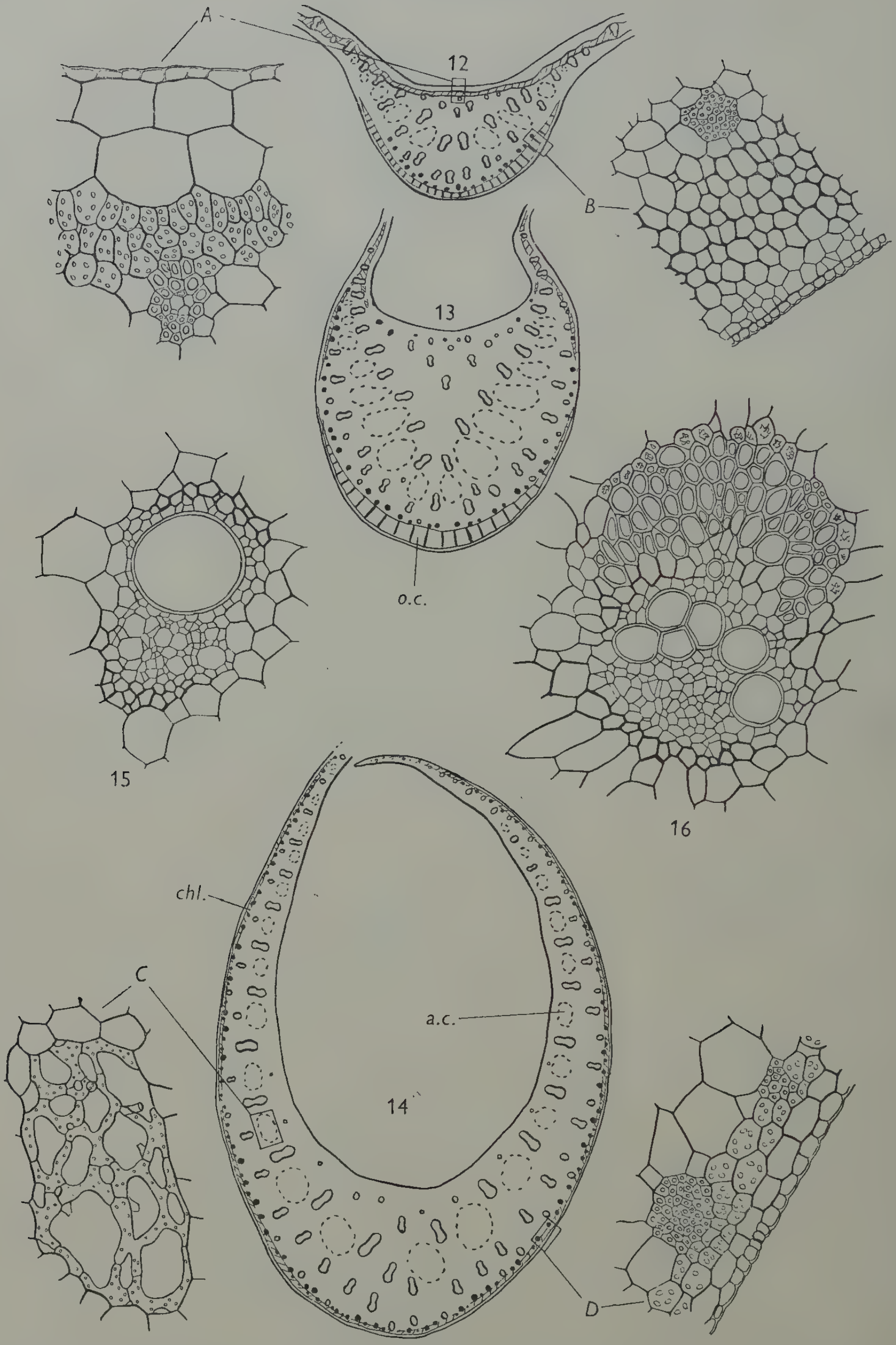
Leaf

Lamina. Dorsiventral or occasionally somewhat isolateral. **Hairs** absent. **Epidermis** with a very thin cuticle, anticlinal walls not sinuous in surface view, slightly thicker than those of mesophyll cells, outermost wall scarcely thicker than inner epidermal walls. Adaxial epidermis (Fig. 1) with costal bands of small, slightly transversely-extended cells differentiated above the few large veins and very wide intercostal bands composed of irregular files of narrow, rectangular, longitudinally-extended cells alternating with single, or sometimes double files of transversely-extended cells, appearing in transverse section as alternate wide and narrow cells (Fig. 5). Abaxial epidermis (Fig. 2) less regular and with more frequent narrow costal bands than the adaxial epidermis; including a coarse crystal sand in *C. coccinea.* **Stomata**: occasional on the adaxial surface but always most frequent abaxially and restricted to the files of transversely-extended cells; terminal subsidiary cells not differentiated, each stoma with a pair of narrow lateral subsidiary cells (Fig. 2); guard cells (Fig. 4) 30–40μ long, each with two cutinized ledges above distinct wall thickenings, inner ledge sometimes distinctly smaller than outer ledge as in *C. indica.* **Hypodermis** (Figs. 3, 5) 1-layered beneath each surface, cells thin-walled, colourless, transversely extended, rectangular or hexagonal; abaxial hypodermis shallower than adaxial and interrupted by wide substomatal chambers, chambers not surrounded by regularly arranged cells. Adaxial hypodermal cells said by Löv (1926) to serve as expansion cells. **Chlorenchyma** always with a distinct adaxial palisade but the layer of chlorenchyma cells adjacent to the abaxial hypodermis sometimes palisade-like, as observed in *C. orientalis*; abaxial mesophyll layers otherwise loose, often lobed and extending across the substomatal chambers. **Veins** rather diffuse; a few large veins (Fig. 7) attached by fibres to both surfaces but separated from epidermis by files of small silica-cells; smaller veins (Fig. 3) either attached to each hypodermis or attached to abaxial hypodermis only; smallest veins in the mesophyll, independent of surface layers. Most veins each sheathed laterally by a single layer of colourless parenchyma; smallest veins rarely completely sheathed by parenchyma; fibrous buttresses well developed above and below larger veins (Fig. 7) but fibres associated with the smaller veins often restricted to the lower side and fibres sometimes completely absent from around the smallest veins. Largest veins (Fig. 7) each with a single wide, tracheal element, adaxial extended protoxylem and abaxial, narrow late metaxylem elements. Xylem of smaller veins much reduced. **Transverse commissures** (Fig. 6) frequent, equidistant from each surface and sheathed by parenchyma; vascular tissues reduced.

Leaf axis. Midrib (Fig. 12), petiole (Fig. 13) and leaf sheath (Fig. 14) distinct from each other but gradually confluent and not articulate. **Hairs** absent. **Epidermis** very uniform, composed of files of rectangular, longitudinally-extended, slightly thick-walled cells. **Stomata** occasional. '**Oblique cells**' (*Wassergewebe* of German authors) visible externally as a white abaxial band extending along the greater part of the midrib (Fig. 12) but ending abruptly at the junction of lamina and petiole; in transverse section (Fig. 12*B*) forming a thick abaxial arc of regular, hexagonal and slightly thick-walled cells; individual cells long, oblique and resembling the peripheral cells in the pulvini of members of the Marantaceae. Oblique cells absent from an unnamed *Canna* hybrid examined by me. **Air-lacunae** (Figs. 12–14, *a.c.*) arranged in a single arc, each lacuna continuous from the leaf base into the distal part of the midrib, traversed by two types of tissue: (*a*) compact, mostly multiseriate diaphragms of more or less isodiametric cells enclosing small intercellular spaces, sometimes including transverse vascular commissures; (*b*) a very loose tissue of stellate 'algiform' cells (Fig. 14*C*) apparently forming irregular septa but connected to one another by numerous vertically-extended cells; cells in both types of tissue containing very small chloroplasts. **Veins** in leaf axis arranged in several distinct



Figs. 1–11. 1. Adaxial epidermis, surface view (×150). 2. Abaxial epidermis, surface view (×150); crystal sand only drawn in a few cells. 3. T.S. lamina, including two medium-sized veins (×60). 4. T.S. stoma from abaxial surface (×660). 5. T.S. adaxial surface layers of lamina (×250). 6. T.S. transverse commissure of lamina (×250). 7. T.S. main vein of lamina (×150). 8. Starch grains from rhizome (×120). 9. T.S. mucilage canal from internode of aerial stem (×250). 10. Perforation plate from root with two thickening bars (×150). 11. Simple perforation plate of vessel element from root (×150).



Figs. 12–16. 12. T.S. midrib halfway between base and apex of lamina (×6). *A*. Enlargement of adaxial part of midrib (×120). *B*. Enlargement of abaxial part of midrib (×120). 13. T.S. petiole just below insertion of lamina (×6). 14. T.S. sheathing leaf base (×6). *C*. Enlargement of air-canal from leaf sheath (×120). *D*. Enlargement of abaxial part of leaf sheath (×120). 15. T.S. central vascular bundle from internode (×120). 16. T.S. vascular bundle from centre of rhizome (×120); starch grains not drawn. *o.c.*, oblique cells; *a.c.*, air-canal; *chl.*, chlorenchyma.

systems: (I) a single arc of large bundles pectinating with but more or less adaxial to the air-lacunae; (II) an adaxial arc of few, small, often inverted vascular bundles, most conspicuous in the petiole; (III) an abaxial system of medium-sized bundles external to the air-lacunae. Individual bundles of the main arc and larger bundles of the abaxial (III) arc like main arc bundles described in other members of the Scitaminae (e.g. Tomlinson, 1956; fig. 4*a*); smaller bundles of other arcs, including reduced vascular tissues, sometimes completely sheathed by fibres; near leaf insertion bundles said by Solereder & Meyer (1930) (S. & M.) to be sheathed by collenchyma. **Fibrous bundles** forming an abaxial system of large and small pectinating strands close to abaxial surface; largest bundles, often containing a little vascular tissue, pectinating with abaxial vascular bundles. **Chlorenchyma** (Figs. 12–14, *chl.*) always present in midrib as an *adaxial* band (Fig. 12*A*) of 3–4 layers of small rounded cells continuous with chlorenchyma of lamina, separated from the epidermis by 2–3 layers of colourless cells; ending more or less abruptly at the junction of blade and petiole; chlorenchyma in leaf sheath present as an *abaxial* band (Fig. 14*D*) separated from the epidermis by a single colourless hypodermal layer and frequently including abaxial fibrous strands. **Ground parenchyma** uniform, that of petiole sometimes including starch grains.

Stem

Aerial stem. **Epidermis** thinly cutinized; cells rectangular, elongated, walls slightly thickened. **Stomata** occasional.

(i) *Internode.* Boundary between cortex and central cylinder not distinct. **Chlorenchyma** present as 1–2 layers of small cells separated from the epidermis by 1–2 layers of colourless hypodermal cells. **Peripheral vascular bundles** in contact with chlorenchymatous layer and forming a weak mechanical zone made up of a ring of large bundles pectinating with, often large, **fibrous strands**. Large peripheral vascular bundles like those of the main arc (I) of the leaf sheath, each with a well-developed fibrous phloem sheath. **Central vascular bundles** (Fig. 15) irregularly scattered, without sheathing fibres but sometimes with a little thick-walled prosenchyma adjacent to xylem and phloem, each bundle including a single wide tracheal element, only the largest including extended protoxylem. Ground tissue including numerous wide **mucilage canals** (Fig. 9).

(ii) *Node.* Slightly swollen and including a **vascular plexus** of many horizontal, girdling and anastomosing bundles; main leaf traces entering the stem abruptly. Large **mucilage cavities** conspicuous and continuous with mucilage canals of internodes.

Rhizome. **Epidermis** not cutinized, sometimes tanniniferous. **Cortex** fairly narrow, containing scattered vascular bundles each with fibres adjacent to xylem and especially phloem. Cortical fibrous strands sometimes present according to S. & M. **Central cylinder** delimited from cortex by a very indistinct endodermis surrounding a narrow zone of small cells which includes girdling and anastomosing vascular strands. Central **vascular bundles** arranged in an irregular manner, each (Fig. 16) with several metaxylem elements, phloem sheathed by fibres with wide lumina. **Mucilage canals** apparently restricted to the periphery of the central cylinder, wider and more irregular than canals in aerial stem.

Course of the vascular bundles in the stem. Main leaf traces said by Falkenburg (1876) to have the ‘palm type’ of distribution in the stem. The nodal plexus is not mentioned by this author. Rhizome similar but leaf traces inserted almost horizontally; system of cortical bundles in rhizome independent of vascular system of central cylinder according to Guillaud (1878).

Root

Piliferous layer shrivelled and eroding from mature roots. **Cortex** including compact peripheral layers of small, slightly suberized cells, hexagonal in transverse section, described as an 'Exodermis' by S. & M.; inner cortex very uniform, cells arranged in radial and concentric files and including very uniform intercellular spaces, innermost 1–2 layers adjacent to endodermis sometimes thick-walled. **Endodermis** with slight U-shaped thickenings in mature roots but, in unstained sections of young roots, sometimes difficult to distinguish from thick-walled cells on either side. **Pericycle** 1-layered. **Stele** with typical polyarch arrangement of vascular tissues, radial files of tracheal elements sometimes V-shaped in transverse section; a central wide vessel recorded by S. & M. in roots of *C. indica* but never observed by me. Ground tissue thick-walled, not medullated.

Secretory elements and cell inclusions

Silica common as druse-like stellate bodies in all parts of the plant except the root; each in a small thin-walled cell, the cells always in long continuous files adjacent to the fibres of the vascular bundle sheaths. Silica-cells homologous with stegmata of other members of the Scitamineae.

Crystals of calcium oxalate common in the ground tissue of all parts except the root; crystals rhombohedral, often forming a coarse sand like that observed in the abaxial epidermis of *C. coccinea* (Fig. 2).

Tannin common in unmodified parenchyma cells, recorded from all parts but most frequent in the stem.

Starch (Fig. 8) abundant in ground parenchyma of rhizome; grains flattened elliptical, eccentric, striated, mostly 60–90μ long, but up to 130μ long in rhizome of *C. edulis* and *C. indica*.

Anthocyanin in vacuoles of epidermal cells imparting a reddish colour to aerial parts of some species.

Mucilage, said to include cystalline material (Szabó, 1881), exuding at cut surfaces from **mucilage canals** in aerial stem and rhizome. Canals in aerial stem long, branched and anastomosing, widening into cavities at the nodes; rhizome canals wider and less regular. Each canal (Fig. 9) with a central mucilage-filled cavity surrounded by small secretory cells which may protrude into the cavity. Lysigenous development of canals recorded by Lutz (1897), but possibility of schizogenous development indicated by Leblois (1887). Development of cavities in the phloem of the vascular bundles recorded by Lutz.

Albuminous crystals recorded by S. &. M. in chloroplasts in rhizome of *C. gigantea* and in leucoplasts of scale leaves of *C. warscewiczii*.

Vascular elements

Vessels present only in the root; elements 1100–2500μ long, 80–130μ wide with simple (Fig. 11) perforation plates on transverse or slightly oblique end-walls, plates sometimes scalariform with few thickening bars (Fig. 10). Elements in aerial stem possibly perforated but if so end-walls scarcely different from those of imperforate tracheids. **Tracheids** in other organs usually without true end-walls, with scalariform pitting.

Seedling development and anatomy

This has been described in some detail by Gérard (1881) and Gatin (1908).

DISCUSSION

Until the anatomy of the Marantaceae has been described and so the present survey of the anatomy of the Scitamineae completed it is not possible to compare *Canna* fully with allied families. However, a few of the more obvious points of comparison which have come to light in the present work may be mentioned. First it is obvious that in addition to its distinct morphological characters (p. 467), *Canna* can be recognized in the vegetative state because it possesses several structural features not found in other members of the Scitamineae. On the other hand, it shares many common features with related families, particularly the rhizomatous types, but not in such a way as to suggest that any one of these is more closely related to *Canna* than is any other. These observations are summarized below.

(i) *Structural features restricted to* Canna

(*a*) Epidermis composed of alternating files of wide and narrow cells.

(*b*) Abaxial tissue of 'oblique cells' present in the petiole. (This tissue is sometimes absent; a similar tissue is found in the Marantaceae but its distribution is quite different.)

(*c*) Algiform cells of air-canals in leaf axis containing small chloroplasts.

(*d*) Aerial stem without a clear boundary between cortex and central cylinder or a well-marked peripheral mechanical zone.

(*e*) Mucilage canals abundant in aerial stem and rhizome.

(ii) *Distribution of some structural features common to* Canna *and other Scitaminean families*

(*a*) Hairs absent. (*Heliconia*, *Musa*, Lowiaceae, Strelitziaceae.)

(*b*) Hypodermis of lamina 1-layered beneath each surface. (*Heliconia*, Lowiaceae, most Marantaceae and Zingiberaceae.)

(*c*) Veins of lamina equidistant from each surface and rarely attached to surface layers by fibrous buttresses; parenchyma of bundle sheath usually 1-layered. (*Heliconia*, most Marantaceae and Zingiberaceae.)

(*d*) Air-canals of leaf axis arranged in a single arc at all levels. (*Musa*, Zingiberaceae, most Marantaceae.)

(*e*) Tissue of 'oblique cells' present in leaf axis. (Marantaceae, but distribution quite different.)

(*f*) Nodal vascular plexus in well-developed aerial stem. (*Costus*, Marantaceae.)

(*g*) Starch grains flattened. (*Musa*, Strelitziaceae, some Zingiberaceae.)

(*h*) Druse-shaped silica-bodies in thin-walled silica cells (stegmata). (*Costus*, Strelitziaceae.)

(*i*) Distribution of silica-cells. (*Costus*.)

(*j*) Distribution of vessels. (As in most rhizomatous Scitamineae.)

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The Genus *Pycnolejeunea* and its affinities to *Cheilolejeunea, Euosmolejeunea, Nipponolejeunea, Tuyamaella, Siphonolejeunea* and *Strepsilejeunea*

By P. KACHROO
Indian Council of Agricultural Research, New Delhi

and R. M. SCHUSTER
Department of Botany, University of Massachusetts

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INTRODUCTION

The genus *Pycnolejeunea*, as it is understood (we are tempted to state misunderstood) in the extant literature, sharply exemplifies the present chaotic condition of the taxonomy of the Lejeuneaceae; for example the genus was recently 'monographed' for Indo-Malaya by Hoffmann (1935)—yet only a very few of the species cited by Hoffmann, that we have studied, appear to belong to *Pycnolejeunea*! Species of *Pycnolejeunea* have been described in the last five decades by a variety of authors, among them Stephani, Schiffner, Herzog, Hattori and others. Yet, since the group was first established by Spruce (1884–85) as a subgenus, only Evans (1906) has had any clear concept of the genus! It appears hardly possible that after the careful scrutiny of the genus by Evans the group could have undergone such an involved and erroneous history as that outlined below.

These erroneous concepts of *Pycnolejeunea*, dating from the year (1893) of its establishment as a genus, have involved largely the six genera we list in the title: *Nipponolejeunea, Tuyamaella, Siphonolejeunea, Cheilolejeunea, Euosmolejeunea* and *Strepsilejeunea*. In order to clarify this discussion and to serve as a means of orientation, a key to these taxa is given below, followed by a diagnosis of the genus *Pycnolejeunea*, and a discussion of its affinities (at times remote) to each of these genera. In conclusion, an attempt is made to arrange the species erroneously referred to *Pycnolejeunea* into their proper genera.

KEY TO *PYCNOLEJEUNEA* AND THE GENERA (AND SUBGENERA) COMMONLY CONFUSED WITH IT

1. Lobe and lobule longly inserted on the axis; lobuli with a single apical tooth, the hyaline papilla marginal; asexual propagation by means of discoid gemmae absent. 2

2. The hyaline papilla proximal, the apical tooth one-celled, blunt or occasionally acute; lobuli obovate, elongate-lingulate, or ovate and greatly inflated; or utriculate, inflated and dilated throughout. Leaves densely imbricate usually with rounded apices, rarely apiculate, deflexed; usually with ocelli; underleaves normally broader than long, usually densely imbricate; stem anatomy various; perianth usually somewhat compressed, rarely terete; microphyllous shoots often developed; caducous leaves never developed. *Pycnolejeunea* s.lat. *a*

a. Perianth often compressed, keels sharp, the beak terminal; leaf apices rounded; cells with coarse, prominent, subconfluent trigones, strongly convex; lobuli variable, but always inflated, at least along the keel; stem with 7–14 rows of cortical cells, the ventral merophytes 2–4 cells wide; bracts entire-margined; microphyllous shoots often developed; plants firm in texture, often brown when dry. Subg. *Pycnolejeunea*

a. Perianth terete in cross-section, the five carinae inflated, dilated above, produced as crests distally, the beak thus recessed; underleaves strongly cordate at base, the margin and apices reflexed; bracts and bracteole dentate; leaf-apices apiculate; lobule obliquely rectangular, weakly inflated along the keel; without microphyllous shoots; leaf cells thin-walled, plane, without trigones, hexagonal; stem holostipous, cortical cells in 20–22 rows, the ventral merophytes *ca*. 6 cells wide; plants delicate; pale green when dry. Subg. *Perilejeunea*

2. The hyaline papilla distad of apical tooth; lobuli ovoid to flask-shaped to narrowly ovoid, usually with a sharp apical tooth; underleaves infrequently distinctly broader than long; leaves and underleaves never densely imbricate; usually without ocelli; microphyllous shoots absent; stem anatomy normally schizostipous, rarely holostipous; perianths basically 5-carinate, but often the antical keel low and broad or vestigial, the postical carinae often obtuse and coalescent; caducous leaves sometimes present. *a*

a. Leaf lobes broadly rounded at apex; lobes of female bracts rounded to blunt at apex, their lobuli well developed. *Cheilolejeunea* s.lat. *b*

b. Lobuli usually broad and rather short, rarely (on stem leaves) over 0·5 the length of lobe, at the apex always with a 1-celled apical tooth; the distal hyaline papilla in a discrete notch; ocelli absent. *c*

c. Apical tooth sharply differentiated, acuminate, 3–6 times longer than broad; underleaves always small, usually cuneate at base, remote, up to twice as broad as stem; often with caducous leaves. Subg. *Cheilolejeunea*

c. Apical tooth short and blunt, hardly differentiated, 1–2 times as long as broad; underleaves commonly large, contiguous to imbricate, usually rounded to cordate at base, usually 3–5 times as broad as stem; rarely with caducous leaves. Subg. *Euosmolejeunea*

b. Lobuli usually narrow and slender, 0·6–0·8 the length of lobe, the apical tooth prominent, two to several cells long, formed of hardly or moderately elongated cells; underleaves small to remote; ocelli usually absent.[1] Subg. *Xenolejeuna*

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[1] This statement is based on the species we examined. However, *C. vittata* shows about four longitudinal rows of thick-walled cells in the basal half of the leaf, and *C. falsinervis* a longitudinal row, 1-cell broad, extending from near the base for nearly two-thirds the length of lobe.

a. Leaf lobes deflexed, acute to longly apiculate; female bracts with lobes similarly acute to longly apiculate, with obsolete lobuli. *Strepsilejeunea*

1. Lobe and lobule very narrowly inserted on the axis; asexual propagation usually by means of discoid gemmae. 3

3. The apical tooth of lobule single, usually undefined; the hyaline papilla marginal and terminal; lobuli narrow, linear to lanceolate-tubular; leaves narrowly obovate to ovate-lanceolate; cells leptodermous, with trigones; underleaves lobed near to base, lobes erect to suberect, lanceolate to linear, pointed; rhizoid-initial discs prominent; female bracts elongate-lingulate to linear-obovoid; perianth not compressed; stem typically schizostipous; discoid gemmae on leaf lobes developed. *Siphonolejeunea*

3. Lobuli bidentate, the hyaline papilla entally displaced, situated under the base of the apical tooth. 4

4. Stem anatomy holostipous; perianth sharply 3-carinate; leaf-margins, at least locally, developing long uniseriate cilia; underleaves subrotundate, slightly emarginate; asexual reproduction unknown; female bracts with a strongly convex, tectate keel, bracteoles free. *Nipponolejeunea*

4. Stem anatomy typically schizostipous, perianth basically 5-carinate; leaf-margins never developing cilia; asexual reproduction by means of discoid gemmae; underleaves bilobed, often deeply so; female bracts without a tectate keel, bracteole adnate to one of the bracts at base. *Tuyamaella*

PYCNOLEJEUNEA SENSU HOFFMANN (1935)

From the preceding key it is evident that the genus *Pycnolejeunea*, as defined in the recent literature, has been a chaotic admixture of unrelated taxa. In attempting to circumscribe the genus we have found that three wholly different types of species are currently assigned to it: (*a*) species with the lobule unidentate, the hyaline papilla situated at the proximal base of the tooth (*P. spruceana*, *P. schwaneckei*, *P. macroloba*, *P. papulosa*, *P. callosa*, etc.); (*b*) species with the lobule unidentate but the tooth usually sharp and often long, with the hyaline papilla at its distal base (*P. discoidea*, *P. incisa*, *P. longiloba*, *P. imbricata*, *P. ceylanica*, *P. tosana*, *P. trapezia*, *P. micholitzii*, etc.); and (*c*) species with the lobule bidentate, the hyaline papilla ental, at the base of the distal of the two teeth (*P. molischii*, *P. pilifera*, *P. angulistipa*, and *P. appendiculata*).

The circumscription of the genus can be simplified, at once, if the species of the group *c* are removed. Hattori (1944, 1947) proposed the genera *Tuyamaella* with *P. molischii* as the generic type and *Nipponolejeunea* with *P. pilifera* as the generic type. These genera are very well defined, indeed. Their species differ from *Pycnolejeunea* s.str., not only in the two teeth of the lobule, and the ental position of the hyaline papilla, but also in the distinctive insertion of the lobule and the lobe on the stem. *Tuyamaella* and *Nipponolejeunea* approach the otherwise unrelated genus *Diplasiolejeunea* in this respect.[1]

We wish to point out that the nature of the leaf-insertion in the Lejeuneaceae is perhaps the most important single character as regards the grouping of the various series of genera. It is, further, our contention that a single type of leaf-insertion characterizes each major group or subfamily of Lejeuneaceae. Spruce (1884, p. 65) long ago emphasized the fact that in the Lejeuneaceae as a whole, 'each leaf is inserted on the stem on two lines meeting below at an angle resembling a narrow letter V, and diverging but slightly from

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[1] Herzog (1950; p. 65) proposed the subgenus *Doliolejeunea* as a subgenus of *Pycnolejeunea*, for these species, as well as for *P. jackii* Steph., *P. amboinensis* Schiffn. and *P. utriculata* Steph. However, *Doliolejeunea* is simply a synonym of *Tuyamaella*; *P. pilifera* Steph. is the generic type of *Nipponolejeunea* Hattori, and *P. utriculata* is a good *Pycnolejeunea*. (We have not studied *P. jackii* and *P. amboinensis*.)

parallelism to the axis of the stem—the lobule on the lower line, the lobe on the upper.... This is indeed the typical mode of leaf-insertion throughout the genus [i.e. the family; Spruce placed all genera of Lejeuneaceae in the portmanteau genus *Lejeunea*], with such differences as are induced by the lobule being very much smaller than the lobe, or becoming obsolete, and sometimes by the nearly transverse insertion of the lobe on the stem. The latter character is, however, very rare, and never so marked as obtains throughout the genus *Frullania*, if we except the small subgenus *Cololejeunea*, where the leaf is inserted on an exceedingly narrow base....' Schuster (1955, p. 124) emphasized this '*exceedingly short line of insertion*' (italics his) as a primary character of the subfamily Paradoxae, while the other two subfamilies (Schizostipae and Holostipae) were described as with the 'lobule, as well as lobe,...broadly attached to the stem'. The significance of these differences in leaf-insertion have been generally overlooked in the past. It is surprising that, after the acute observations of Spruce, such authors as Stephani, Schiffner, Herzog and Hoffmann placed species with these radically distinct patterns of leaf attachment into the single 'genus' *Pycnolejeunea*. In an understanding of the classification of the Lejeuneaceae, it is very important to realize that *Tuyamaella* and *Nipponolejeunea*, and the allied genus *Siphonolejeunea*, possess not only the leaf-insertion of Paradoxae, but have a fundamentally identical type of lobule, except only *Siphonolejeunea*, which has a derivative lobule. We consider this correlation to be significant taxonomically and would, therefore, separate the preceding group of three genera from the Schizostipae, to which they appear to possess only a remote affinity. In spite of the similar lobule-type and leaf-insertion, these genera are not immediately allied to the Paradoxae, since the vegetative axes in these taxa possess the ordinary helical segmentation of the Schizostipae and Holostipae, rather than the pendulum-like segmentation of the Paradoxae. The entire problem of the classification of these four genera is dealt with in detail in another connexion (Schuster & Kachroo, 1960). At this point we wish to emphasize merely that these genera, possessing lobule type *c*, as outlined above, bear no affinity to the groups with lobule types *a* and *b*. The latter two groups possess the ordinary J or U-shaped leaf-insertion typical of the 'normal' Schizostipae.

Eliminating the taxa allied to *Nipponolejeunea* and *Tuyamaella* we are still left with groups *a* and *b*. We believe that the lobular structure definitely eliminates the possibility that these two groups belong to a single genus. As a consequence, the primary task with which we are immediately confronted is to decide to which group the generic type belongs. As Evans (1906) pointed out, the derivation of a generic type for *Pycnolejeunea* is a difficult matter. Spruce (1884–85) listed as the first species of his subgenus *Pycnolejeunea*, *Lejeunea contigua* Nees. However, his plants were shown to be unrelated to *L. contigua* Nees, which Stephani (1914, p. 585) placed in *Euosmolejeunea*. Schiffner (1897, p. 583) therefore renamed *L. contigua* Spr., nec Nees, *P. spruceana*. This species, whatever its name, is the first taxon listed under *Pycnolejeunea*, and Evans (1906) with some justification considers it to be the generic type. He has been followed in this by Vanden Berghen (1948), and we accept this as the only rational generic designation. It is somewhat ironic that Stephani at no point in his *Species Hepaticarum* alludes to this species. The only other candidate for the position of generic type is *P. macroloba* (Mont.) Spr. ex Schiffner (not *P. macroloba* (Mont.) Steph., as Stephani, 1914, p. 607 puts it), the species cited under the name *Pycnolejeunea*, as genus, in Schiffner (1893). We suggest that Evans be followed in considering *P. spruceana* as the generic type.

The material of *P.* '*contigua*' studied by us has the lobule of the type *a*; in other words, the hyaline papilla is proximal of the apical tooth, agreeing in this respect with *P. papulosa*, *P. schwaneckei*, *P. macroloba* and *P. callosa*. We suggest, therefore, restricting the name *Pycnolejeunea* to the species with a proximal hyaline papilla. There remains to consider only the species with the hyaline papilla situated distal to the apical tooth, as in *P. discoidea*, *P. incisa*, *P. imbricata*, *P. ceylanica*, *P. tosana* and *P. meyeniana*, etc. These species, for reasons given below, probably are all best assigned to a subgenus of *Cheilo-*

lejeunea, with which they agree in the fundamental structure of the lobule, perianth, underleaf-form, and other primary morphological criteria.

These two groups of species, i.e. those with a proximal hyaline papilla, and those with a distal one, are best treated wholly separately, as below.

TAXA POSSESSING A PROXIMAL HYALINE PAPILLA: *PYCNOLEJEUNEA* (SPR.) SCHIFFN., S.STR.

Lejeunea Hampe & Gottsche, 1852, *Linnaea*, **25**, 356; Mont, 1843, *Ann. Sci. Nat. Bot.*, II, **19**, 260; G. L. & N., 1845, *Syn. Hep.* p. 359 (p.p.).

Lejeunea subg. *Pycno-Lejeunea* Spruce, 1884–85, *Trans. & Proc. Bot. Soc., Edinb.*, **15**, 245–7.

Pycnolejeunea Schiffner, 1893, in Engler-Prantl, *Natur. Pflanzenfam.*, **1** (3), 124; Evans, 1906, *Bull. Torrey Bot. Cl.* **33**, 19–20.

Plants medium-sized to robust, about 1·1–2·5 mm. wide, forming depressed, often compact, prostrate mats, loosely or closely appressed to substrate; green or light green but when dry or dead ± brownish, not glossy; rather profusely irregularly pinnately branched, all branches of the *Radula*-type, occasionally microphyllous shoots developed. Stem pale green to brownish, with variable number of cortical and medullary cell-rows; the cortex with 7–13 (22) cell-rows, the medulla with 10–46 cell-rows and the ventral merophytes 2 to 4 to 6 cell-rows broad (for details see Table 1); the cortical and medullary cells equally strongly thickened, with conspicuous pits in the medullary cells; rarely all cells rather thin-walled. Leaves densely imbricate, not convolute when dry, spreading, often slightly squarrose; lobe subrotundate to oblong-ovate or broadly falcate-ovate, convex, apex rounded, usually decurved; margin entire, occasionally obscurely crenulate due to the convexity of the cells; base weakly to moderately rounded, usually extending across and beyond the axis, inserted on a rather long oblique line. Lobuli variable from

Table 1. *A comparison of some primary characters of the various species of* Pycnolejeunea *s.str.*

Species	Cortical cell-rows	Ventral merophytes in cell-rows	Width of under-leaves:stem	Lobule type	Ocelli
P. decurviloba	12–13	4	5–6:1	Small, deflexed, opening obliquely, curved backwards	None
P. bidentula	7	2	3·5:1	Similar	Few
P. utriculata	7	2	2·9:1	Large, ovate-obovate, inflated and dilated throughout, the free margin revolute from base to apex	None
P. ventricosa	7	2	5·3:1	More or less similar	Few
P. spruceana	7	2	3–4:1	Short, inflated, not deflexed, opening distal	Few
P. papulosa	7	2	5–6:1	Similar	None
P. multiflora	7	2	5·2:1	Similar	Few
P. decurvifolia	7	2	5·5:1	Similar	Few
P. malaccensis	7	2	3–4:1	Similar	None
P. novoguineensis	7	2	4:1	Similar	None
P. sphaeroides	14	3	3·9:1	Similar	Few
P. renistipula	12–14	3	4:1	Similar	Few
P. schwaneckei	13	(3)–4	2·5–3:1	Long, lingulate, not deflexed, opening distal	Many
P. soleniloba	10	2	3–4:1	Similar	Few
P. borneensis	7–9	2	4:1	Similar	Few
P. macroloba	7	2	2·5–3:1	Similar	Few

one section of the genus to the next, of three basic types: (1) narrow, 0·6–0·8 the length of lobe, oblong to oblong-lingulate, inflated chiefly along the keel with free margin appressed to lobe, the sinus moderately to strongly oblique with respect to the posterior lobe margin; (2) short, 0·25–0·35 the length of lobe, weakly or subglobosely inflated in proximal two-thirds, with only the distal portion constricted and narrowed, the narrow sinus at nearly a right-angle to posterior lobe margin; (3) short, 0·2–0·25 the length of lobe, only the basal one-fourth to one-third gibbously inflated, the distal two-thirds compressed, the apex ± reflexed and with aperture directed obliquely backward (see key to sections); lobule with a single, 1-celled, short, blunt to slightly pointed apical tooth; hyaline papilla at proximal base of apical tooth; sinus variable, either short and slightly concave (then only *ca.* 2–3 cells wide, from keel to the apical tooth) and lying at *ca.* an 80–140° angle with posterior lobe margin; or else longer (5–6 cells from base of apical tooth to sinus), and the sinus somewhat oblique to lobe margin (at *ca.* a 40–50° angle to lobe margin). Leaf-cells usually convex, usually with strongly developed trigones; rarely trigones confluent; intermediate thickenings normally absent, infrequently present; cells only exceptionally thin-walled, with trigones minute to indistinct. Ocelli usually present, scattered or restricted to near base of lobe. Underleaves very large, closely imbricate, broadly ovate-orbicular to subreniform, 0·5–0·85 the length of lobe, usually conspicuously broader than long, shallowly to deeply bifid, lobes triangular, pointed or blunt, ± erect, sinus acute to obtuse; underleaves entire-margined, occasionally minutely crenulate, inserted on a weakly to strongly arched line. Radicelliferous discs absent, but rhizoid-initial areas often well developed; rhizoids few to numerous. No mode of asexual reproduction known.

Monoecious or dioecious. Gynoecia borne laterally or terminally on ± elongated branches, with 1–2 subfloral innovations; innovations often fertile. Bracts usually as large or larger than leaves, widely to obliquely spreading, unequally bilobed. Lobe broadly obovate to rounded, apex rounded, entire-margined, exceptionally sparingly dentate (in *P. schwaneckei*), with keel entire. Lobule lanceolate to obovate, apex acute to rounded or blunt, variable even in the same inflorescence. Bracteole usually slightly connate with one of the bracts at the base, larger than underleaves, slightly or indistinctly bifid, lobes pointed or blunt. Perianth obovate or obovate-pyriform, apex broad, usually rounded at apex and with a short, distinct beak; perianth ± compressed (except in subg. *Perilejeunea*), 5-carinate, keels sharp or inflated, smooth, not winged, not produced beyond beak; dorsal keel rarely low and obtuse. Androecia terminal on short or elongated lateral shoots, formed of about 4–5 pairs of bracts, the bracts densely imbricate; bracteoles restricted to the base of the spike; diandrous.

Type. *Lejeunea* (*Pycno-Lejeunea*) *contigua* Spruce (nec *Lejeunea contigua* Nees) = *Pycnolejeunea spruceana* Schiffn.

Our concept of this species is based on material from the Gottsche herbarium, from Brazil (*leg.* Martius, labelled '*Lej. contigua* var. *a.* In distr. Paraensi'). This appears to have been the plant Spruce had in mind when he described *L. contigua* Spruce nec Nees, since the first station (and presumably specimen) cited is Para, Brazil. The material, labelled *type*, studied by us, is a fragment in Evans's herbarium at Yale; it is wholly male.

Pycnolejeunea sensu Spruce & Evans is one of the best-defined groups of Schizostipae, distinguishable at once by the combination of features discussed above.

The normally strongly collenchymatous cells, the rigid, rather firm texture, the very dense leaves and underleaves give the plants a quite unmistakable facies. We cannot understand why the genus *Pycnolejeunea* has been so uniformly and thoroughly misunderstood in the entire literature, after the careful delimitation of the group in Spruce (1884–85) and Evans (1906). However, the confusion with respect to the limits of the genus has been so great that the following resumé is necessary.

Pycnolejeunea, sensu Spruce (nec Hoffmann), appears allied only to some species assigned currently to *Trachylejeunea*, with which it shares the following features: (*a*) lobuli with 1-celled apical tooth, at whose proximal base is situated the hyaline papilla;

(*b*) very convex cells with very coarse trigones; (*c*) ocelli often present; (*d*) perianths 5-carinate with carinae not armed; (*e*) lobes with apices deflexed. The plants in both genera are rather firm and robust, and bear strongly imbricate leaves (although those of *Pycnolejeunea* are more markedly imbricate). The two genera differ in a series of features which suggest that they are not immediately related. *Pycnolejeunea* has the gynoecia on long, leafy axes, with one to two innovations developed; in *Trachylejeunea* the gynoecia are on short lateral branches, usually devoid of innovations. *Pycnolejeunea* has merely convex cells (the convexity sometimes slightly thickened); in *Trachylejeunea* the cells are conically elevated as rounded tubercles. *Pycnolejeunea* has uniformly broadly rounded ventral lobes; in *Trachylejeunea*, although the lobes are similarly deflexed at the apices, they vary from acute to acuminate.

The genus *Pycnolejeunea*, as circumscribed above, still remains distressingly polymorphic. We find variations in stem anatomy and in lobule structure that are difficult to reconcile with a single generic type. Yet, the underleaves and the closely imbricate leaves of all the species studied by us give the group an unmistakable unity. The stem anatomy varies from complex, with 12–13 rows of cortical cells surrounding up to 18–22 rows of medullary cells, to typically schizostipous, i.e. with 7 rows of cortical cells surrounding limited rows (*ca.* 12) of medullary cells. In all cases the cortical cells are thick-walled, although less prominently so than the medullary; the ventral merophytes range from 2 to 6 cells broad.

In spite of this extreme variability, it appears unwise to attempt to separate such a habitually similar series of taxa into two or more genera. The most extreme species of those truly referable to *Pycnolejeunea* is *P. grandistipula* G. ex Steph.; this appears separable as a distinct subgenus. The other species we have studied, by contrast, can best be separated into several sections. Both subgenera are discussed below.

Subgenus *Pycnolejeunea*

Plants firm in texture, when dry more or less brownish; occasionally with microphyllous shoots. Stem pale green to brownish; the cortical cells in 7–14 rows, the medullary in 12–22 cell-rows, the ventral merophytes 2 to 4 cell-rows broad; the cortical and medullary cells equally strongly thickened, with conspicuous pits in the medullary. Leaf lobe convex, apex rounded, usually decurved. Lobuli variable: narrow, oblong-lingulate and chiefly inflated along the keel; or short and inflated in the proximal three-fourths or less, either opening towards the apex of lobe or decurved and opening towards the base of the shoot; the apical tooth in all cases 1 cell long. Leaf cells usually convex, with strongly thickened trigones; trigones rarely confluent. Ocelli present. Underleaves plane, densely imbricate, bilobed, lobes triangular, pointed to blunt, inserted on a weakly arched line. Asexual reproduction unknown.

Gynoecia borne terminally on more or less elongated shoots, with 1–2 innovations; innovations often fertile. Bracts and bracteole entire margined. Perianth compressed, 5-carinate, the carinae sharp and smooth, the dorsal keel rarely low and obtuse; apex rounded, with a short beak. Androecia on elongated lateral shoots; bracts diandrous; bracteole restricted to base (Figs. 1, 2, 3 (1–5), 4 (5–11), 5, 6 (1–7, 22–24)).

The species of the subgenus *Pycnolejeunea* include a number of very different types, which deserve segregation into distinct sections. We would found these sections on: (*a*) differences in stem anatomy; (*b*) differences in form and size of underleaves; (*c*) presence or absence of ocelli; and, primarily, on (*d*) the form, shape and orientation of the lobuli, and the form of their apical teeth.

The lobuli are exceedingly variable from one species to the next. Three distinct types occur in the species we have studied: (*a*) the *P. schwaneckei* type, which has the lobule narrow, lingulate to oblong with the sinus long and oblique, gradually running into the lobe margin; lobule inflated chiefly along the keel; (*b*) the *P. papulosa* type, in which the lobule is inflated hemispherically in the basal two-thirds; the lobule as a whole is abbreviated and less than one-third the length of the lobe; (*c*) the *P. decurviloba* type in which the lobule size is no larger than in type *b*, but only the basal one-fourth or one-third is sharply inflated, the remainder appearing pinched-in, being declivous against the lobe and

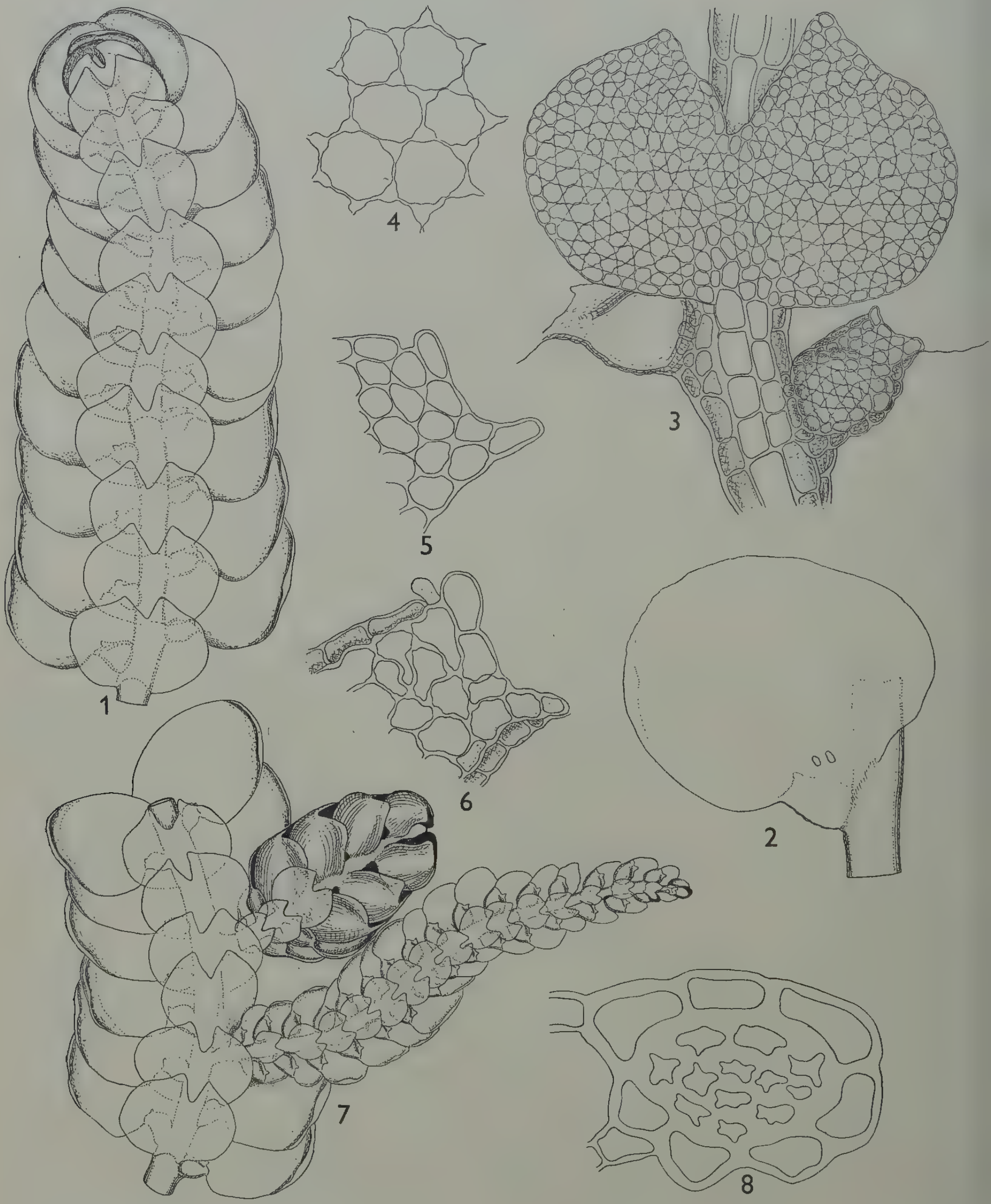


Fig. 1. *Pycnolejeunea spruceana* Schiffn.: 1, sterile shoot, postical view (×40); 2, leaf, antical view (×72); 3, portion of shoot showing underleaf and lobuli and their insertion on axis, postical view (×132); 4, median leaf-cells (×412); 5, apex of lobule (×412); 6, lobule apex, showing proximal hyaline papilla (×412); 7, plant with male spike and microphyllous shoot, postical view (×30); 8, T.S. of stem (×412).

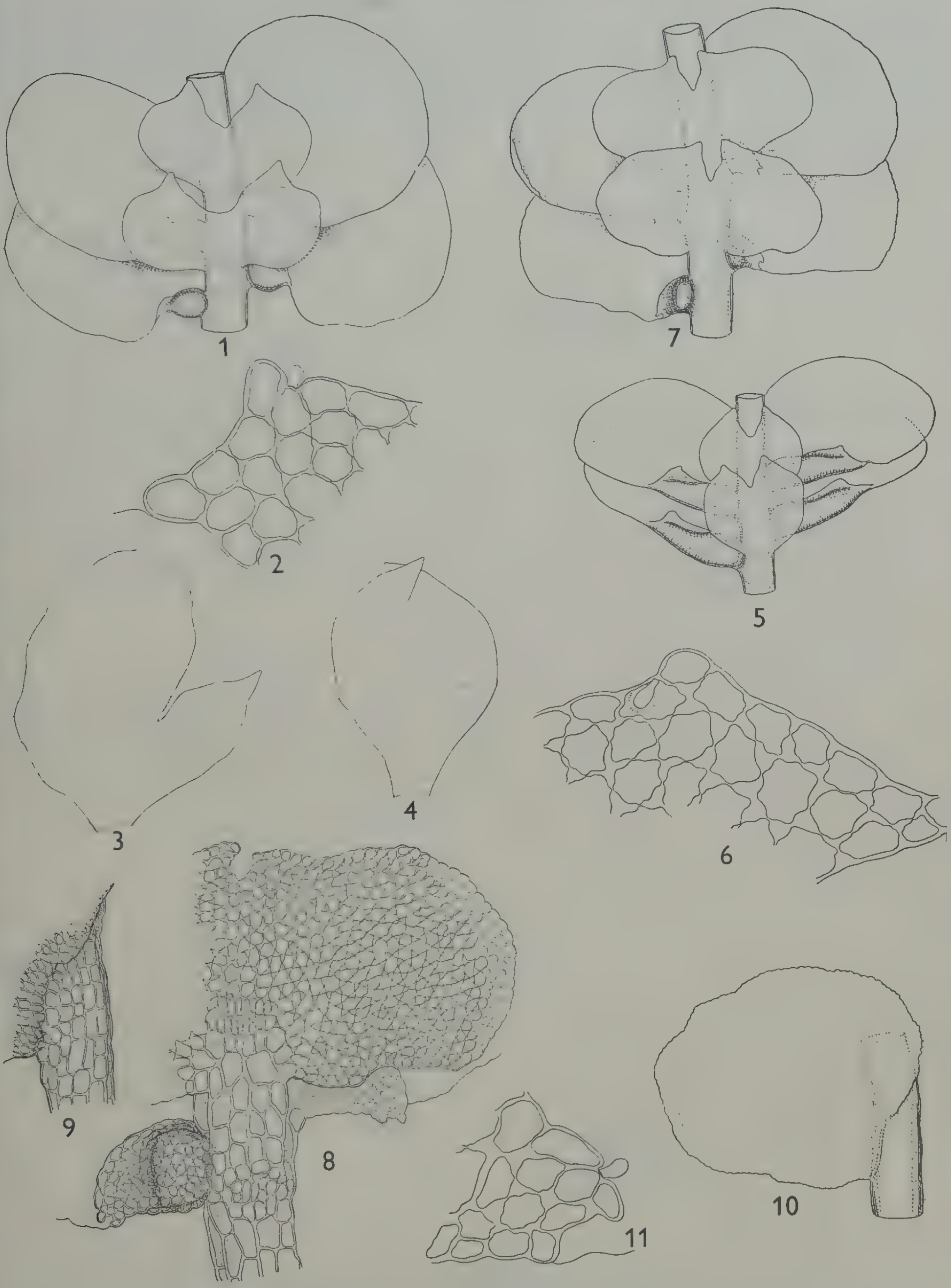


Fig. 2. *Pycnolejeunea papulosa* St.: 1, portion of shoot, postical view (×50); 2, apex of lobule (×412); 3, female bract (×45); 4, bracteole (×45). *P. macroloba* (Mont.) Schiffn.: 5, portion of shoot, postical view (×47); 6, apex of lobule (×412). *P. decurviloba* St.: 7, part of shoot, postical view (×35); 8, same, lobes and a portion of underleaf not drawn (×88); 9, dorsal insertion of leaf on axis (×60); 10, leaf, antical view (×42); 11, apex of lobule (×412).

appressed against it; furthermore, in this type the lobuli are recurved and open obliquely to the back, rather than towards the lobe apices. On the basis of the lobuli and stem anatomy the species of the genus investigated can be divided into distinct complexes, which we believe merit the rank of sections, as shown in the following key. Some of the primary characters of these taxa are also contrasted in Table 1.

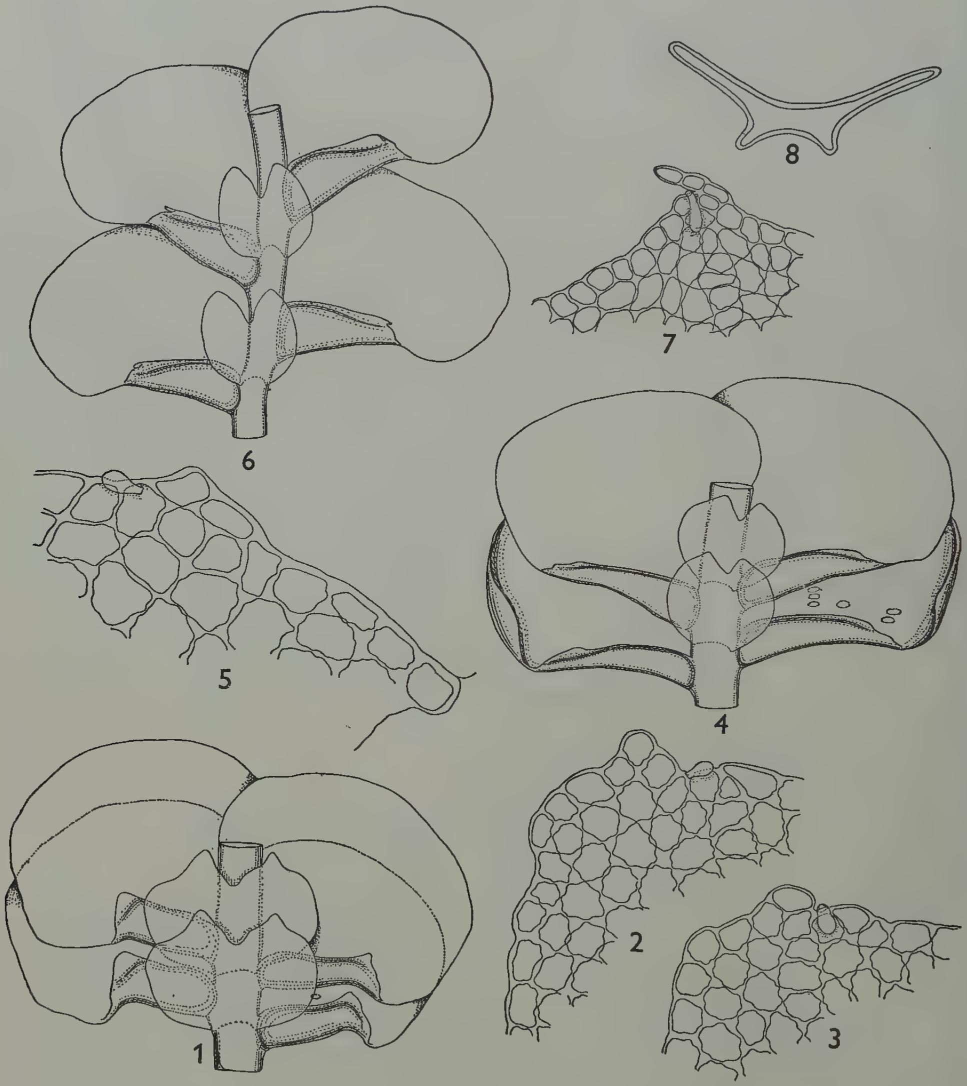


Fig. 3. *Pycnolejeunea callosa* (Ldbg.) St.: 1, part of shoot, postical view (× 50); 2, 3, apices of lobuli (× 400). *P. schwaneckei* (St.) Schiffn.: 4, part of shoot, postical view (× 47); 5, apex of lobule (× 400). *Cheilolejeunea* (*Xenolejeunea*) *imbricata* (Nees) Schuster & Kachroo: 6, part of shoot, postical view (× 47); 7, apex of lobule (× 425); 8, T.S. of perianth (× 62).

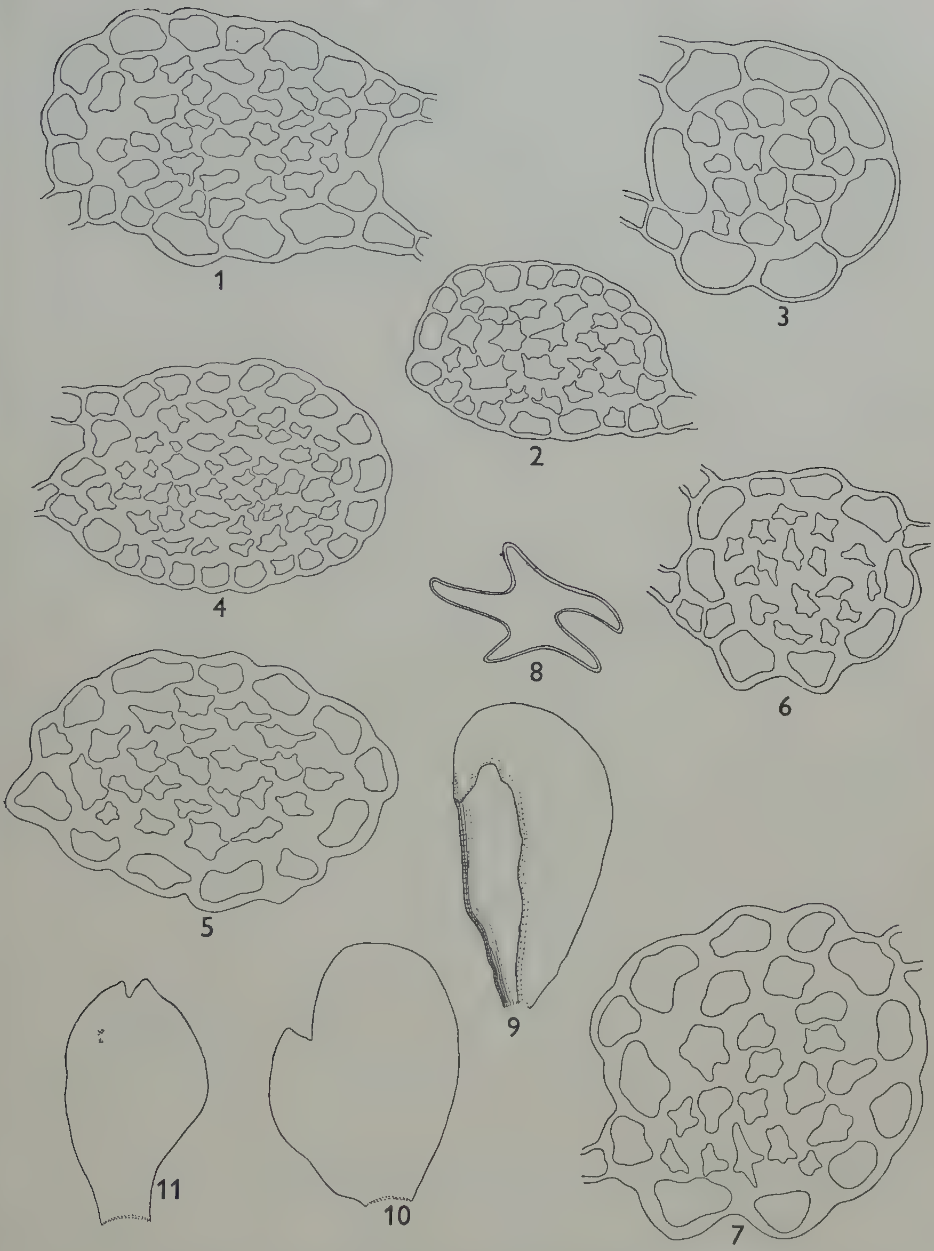


Fig. 4. *Cheilolejeunea* (*Xenolejeunea*) *incisa* (Gottsche) Schuster & Kachroo: 1, T.S. of stem (× 242). *C.* (*X.*) *trapezia* (Nees) Kachroo & Schuster: 2, T.S. of stem (× 310). *C.* (*X.*) *micholitzii* (St.) Kachroo & Schuster: 3, T.S. of stem (× 312). *C.* (*X.*) *imbricata* (Nees) Schuster & Kachroo: 4, T.S. of stem (× 242). *Pycnolejeunea decurviloba* St.: 5, T.S. of stem (× 285); *P. callosa* (Ldbg.) St.: 6, T.S. of stem (× 224). *P. schwaneckei* (St.) Schiffn.: 7, T.S. of stem (× 285); 8, T.S. of perianth (× 25); 9, 10, female bracts (× 45); 11, bracteole (× 45).

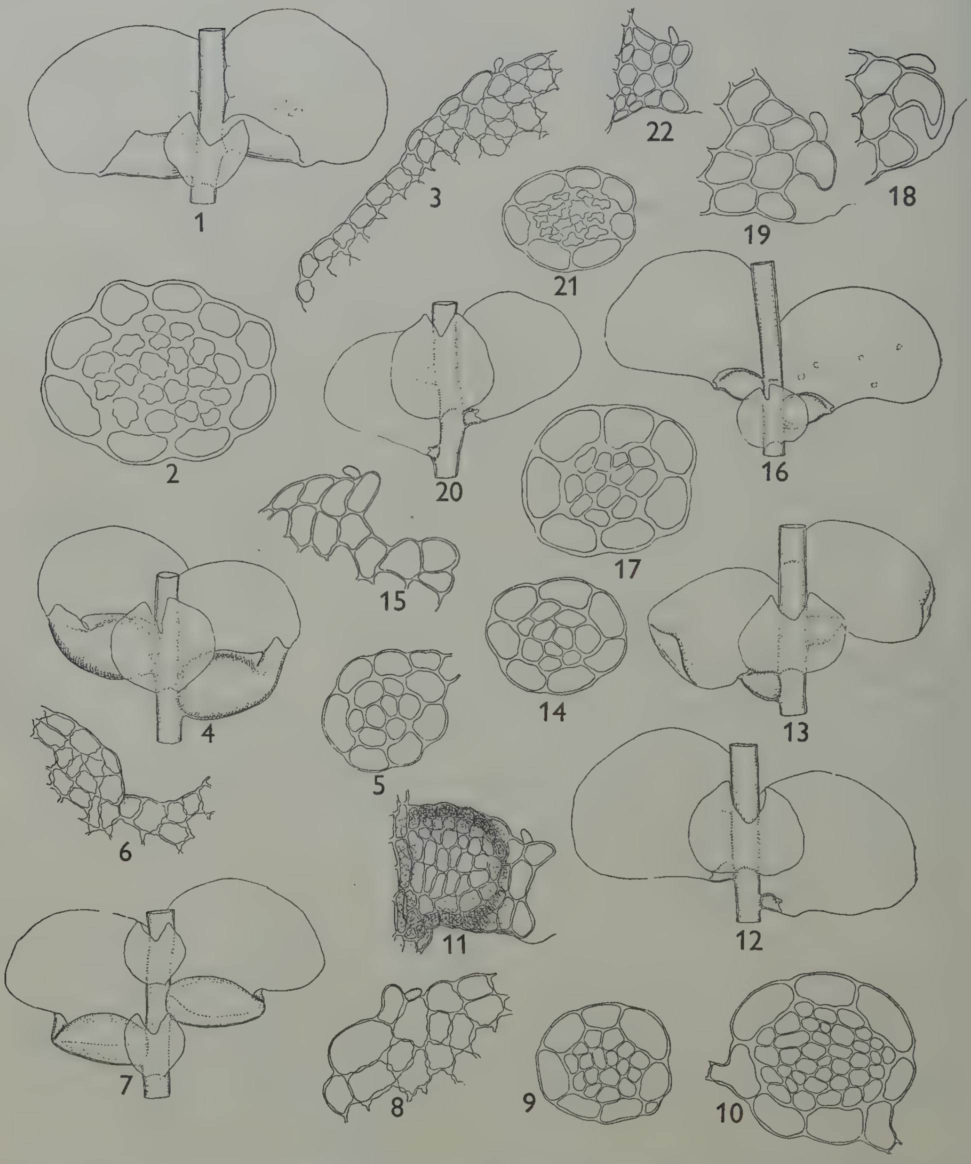


Fig. 5. *Pycnolejeunea borneensis* St.: 1, portion of shoot, postical view (×30); 2, T.S. of stem (×180); 3, apex of lobule showing apical tooth and hyaline papilla (×180). *P. ventricosa* Schiffn.: 4, portion of shoot, postical view (×45); 5, T.S. of stem (×250); 6, apex of lobule (×250). *P. utriculata* St.: 7, portion of shoot, postical view (×32); 8, apex of lobule showing apical tooth and hyaline papilla (×152); 9, T.S. of stem (×152). *P. decurvifolia* St.: 10, T.S. of stem (×185); 11, apex of lobule showing apical tooth and hyaline papilla (×185); 12, portion of shoot, postical view (×22). *P. novoguineensis* St.: 13, portion of shoot, postical view (×50); 14, T.S. of stem (×232); 15, apex of lobule showing apical tooth and hyaline papilla (×232). *P. bidentula* St.: 16, portion of shoot, postical view (×27); 17, T.S. of stem (×212); 18, 19, apices of deflexed lobuli, each showing apical tooth and hyaline papilla (×280). *P. multiflora* St.: 20, portion of shoot, postical view (×35); 21, T.S. of stem (×155); 22, lobule showing apical tooth and hyaline papilla (×155).

Key to sections

1. Lobuli small or very small; length one-eighth to one-third the actual length of lobe. 2

2. Lobuli curved so that the orifice is directed obliquely backward, rather than to lobe apex (the very narrow sinus at an angle of more than 90° to axis); leaves and underleaves densely imbricate. (Marginal cells 18–23 μ; median cells 24–29 μ). 3

3. Cells strongly collenchymatous, with coarse trigones; underleaves very large, broadly transverse, 5–6 times as broad as stem; stem with *ca.* 12–13 rows of cortical cells, the ventral merophytes 4 cells broad; lobuli with only basal fourth strongly inflated, the distal two-thirds or more appearing pinched in. (Marginal cells *ca.* 23 μ; median cells 27–29 μ.) American. Section Decurvilobae (*P. decurviloba*)

3. Cells equally thick-walled; underleaves rather small, one-fifth to one-sixth the area of lobes, three times as broad as stem; stem with 7 rows of cortical cells and 2 rows forming the ventral merophytes; lobuli inflated except near apex, ovoid. (Marginal cells 18–22 μ; median cells 24–27 μ.) South-eastern Asia.
Section Bidentulae (*P. bidentula*; see also *P. decurvifolia*)

2. Lobuli 'normal', ovoid in shape, the orifice directed towards the lobe apex (sinus at an angle of 45–90° to axis). 4

4. Stem with *ca.* 14 rows of cortical cells, the ventral merophytes 3–4 cells broad; cells with trigones not obvious, the walls becoming thickened except for pits; leaves and underleaves densely imbricate. (Marginal cells 16 μ; median cells 23–28 μ.) Asian. Section Sphaeroides (*P. sphaeroides*)

4. Stem with 7 rows, the ventral merophytes 2 cells broad. 5

5. Underleaves exceedingly broad and large: (3)4–6 times the width of stem; their area and width approaching the length and area of lobe; trigones normally coarse and well developed. Leaves and underleaves very closely imbricate. (Marginal cells 18–22 μ; median cells 22–25 μ.) American. Section Spruceanae (*P. spruceana*, *P. papulosa*)

5. Underleaves normally smaller; 3–4, rarely 5 times the width of stem, their width much less than length of lobe; leaves and underleaves varying from contiguous to weakly imbricate. (Marginal cells 13–20 μ; median cells (16)19–28 μ.) Asian. 6

6. Cells equally thick-walled, or nearly so, without obvious trigones and intermediate thickenings; leaves distinctly imbricate, the underleaves slightly to distinctly imbricate or at least contiguous; perianth (where known) somewhat compressed, with antical keel low.
Section Multiflorae (*P. multiflora*, *P. malaccensis*, *P. decurvifolia*)[1]

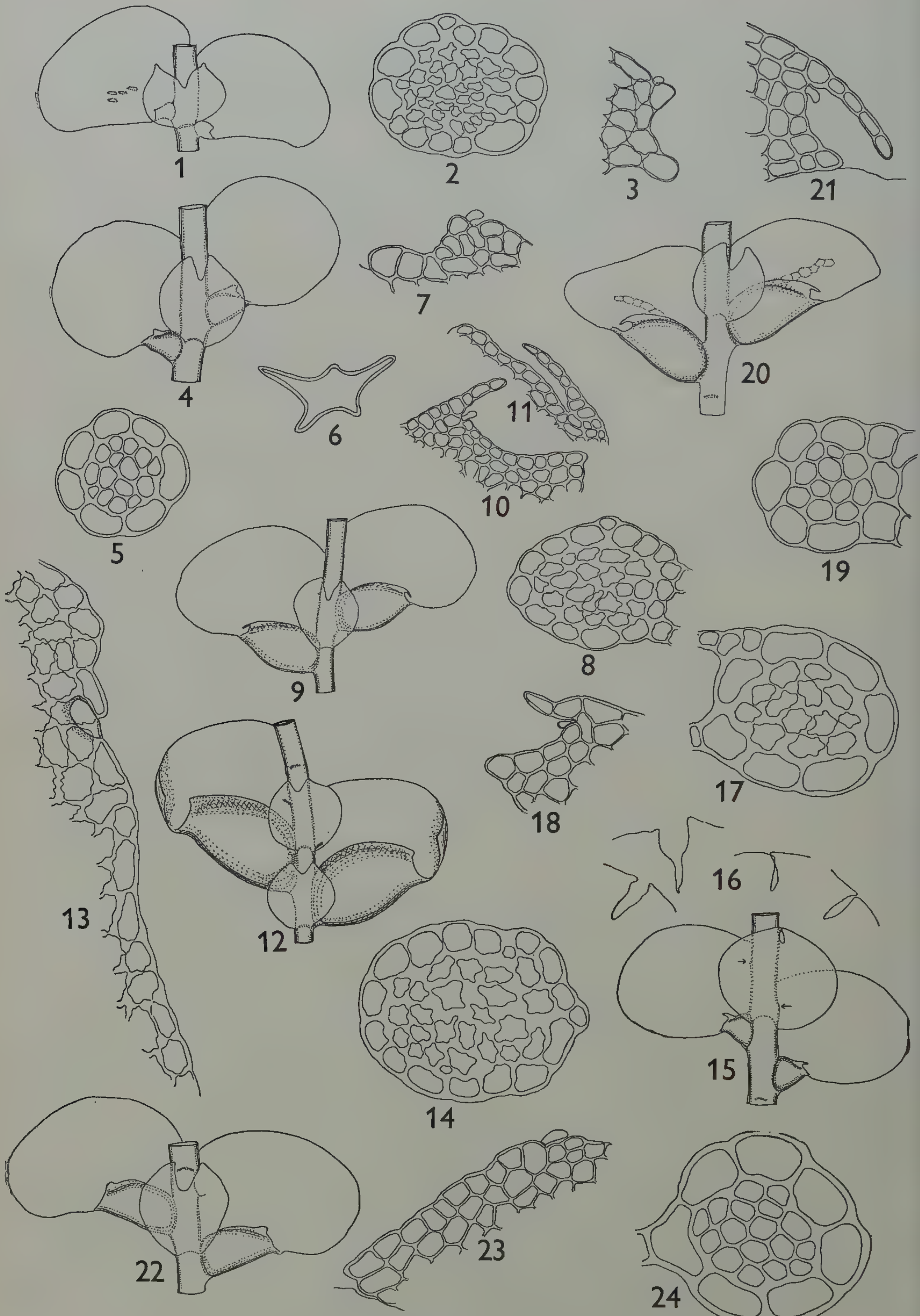
6. Cells thin-walled, with distinct trigones and occasionally intermediate thickenings; leaves barely imbricate or contiguous; underleaves remote to contiguous; perianth terete, not compressed, weakly 5-plicate in distal one-fifth. Section Novoguineenses (*P. novoguineensis*)

1. Lobuli large, their length one-half to four-fifths that of lobe, usually narrow and 3–7 times as long as broad. 7

7. Lobuli inflated essentially throughout, utriculate in nature; underleaves remote to contiguous. Asian.
Section Utriculatae (*P. utriculata*, *P. ventricosa*)

7. Lobuli inflated largely along keel, not ventricose; underleaves ± closely imbricate. American (exc. *P. borneensis*).
Section Macrolobae (*P. macroloba*, *P. schwaneckei*, *P. callosa*, *P. borneensis*)

[1] *P. decurvifolia* has the small lobuli spreading at an angle of over 90°, at times. It approaches the Section Bidentulae and serves to connect *P. bidentula* with the Section Multiflorae.



For legend see facing page.

Key (tentative) to species of the subgenus Pycnolejeunea

1. Lobule small, one-third to one-eighth the length of lobe; apical tooth well defined. **2**

2. Lobule one-third the length of lobe; ocelli often present; cells various. **3**

3. Stem with 7 rows of cortical cells, the ventral merophytes 2 cells wide; underleaves remote to contiguous, 3–4 times as wide as stem; ocelli absent (at least in herbarium specimens examined); lobule normal, the apex not recurved; marginal cells *ca.* 13–17 μ. Asian. **4**

4. Leaf-cells small, marginal cells about 13 μ wide, the median 16–20 μ wide, rather equally thick-walled, trigones indistinct; perianth compressed, 5-carinate, the dorsal keel low, somewhat obtuse, the ventral and lateral keels sharp; plants small, 0·7 mm. wide, rather firm. *P. malaccensis* Steph.

4. Leaf-cells larger, marginal about 17 μ wide, median 25–27 μ wide, cells with coarse trigones, intermediate thickenings present; perianth not compressed, terete, weakly 5-plicate in the distal one-quarter; plants rather delicate, medium-sized, 1·1 mm. wide; underleaves distant (leaves usually contiguous and lobuli obsolete). *P. novoguineensis* Steph.

3. Stem anatomy various;[1] underleaves densely imbricate; ocelli often present; marginal cells 18–23 μ wide. **5**

5. Lobule deflexed, curved backwards, opening towards the posterior margin of lobe, orifice slit-like, narrow, margined by *ca.* 2–3 cells; stem anatomy various; median cells 24–29 μ wide. **6**

6. Leaf-cells equally thick-walled, trigones not distinct; stem with 7 rows of cortical cells, the ventral merophytes 2 cells wide; lobuli inflated except near apex; ocelli few, scattered; underleaf as broad as long, 3 times as wide as stem, sinus sharp; plants about 2·1 mm. wide. Asian. *P. bidentula* Steph.

6. Leaf-cells with large, coarse trigones, the latter often confluent; stem with cortical cells in 12–13 rows, the ventral merophytes 4 cells wide; ocelli absent; lobuli only inflated in the basal one-quarter; underleaves more than twice as broad as long, 5–6 times as wide as stem; sinus shallow; plants 1·5 mm. wide. American. *P. decurviloba* Steph.

Fig. 6. *Pycnolejeunea sphaeroides* St.: 1, portion of shoot, postical view (× 20); 2, T.S. of stem (× 150); 3, apex of lobule showing apical tooth and hyaline papilla (× 150). *P. malaccensis* St.: 4, portion of shoot, postical view (× 45); 5, T.S. of stem (× 235); 6, T.S. of perianth near apex (× 235); 7, apex of lobule with apical tooth and hyaline papilla (× 235). *Cheilolejeunea* (*Xenolejeunea*) *verdoornii* (Hoffm.) Kachroo & Schuster: 8, T.S. of stem (× 150); 9, portion of shoot, postical view (× 20); 10, 11, apices of lobuli, each showing apical tooth and hyaline papilla (× 150). *C.* (*X.*) *gigantea* (St.) Schuster & Kachroo: 12, portion of shoot, postical view (× 12); 13, apex of lobule, showing undefined apical tooth and hyaline papilla (× 195); 14, T.S. of stem (× 167). *C.* (*X.*) *cookiensis* (St.) Schuster & Kachroo: 15, portion of shoot, postical view (× 30); 16, apices of underleaves (× 62); 17, T.S. of stem (× 195); 18, apex of lobule (× 230). *C.* (*X.*) *falsinervis* (St.) Kachroo & Schuster: 19, T.S. of stem (× 285); 20, portion of shoot, postical view (× 50); 21, apex of lobule (× 285). *Pycnolejeunea duissa* (in Farlow herb.): 22, portion of shoot, postical view (× 30); 23, apex of lobule (× 212); 24, T.S. of stem (× 275).

[1] Cortical cells in 7 rows, except in *P. decurviloba*.

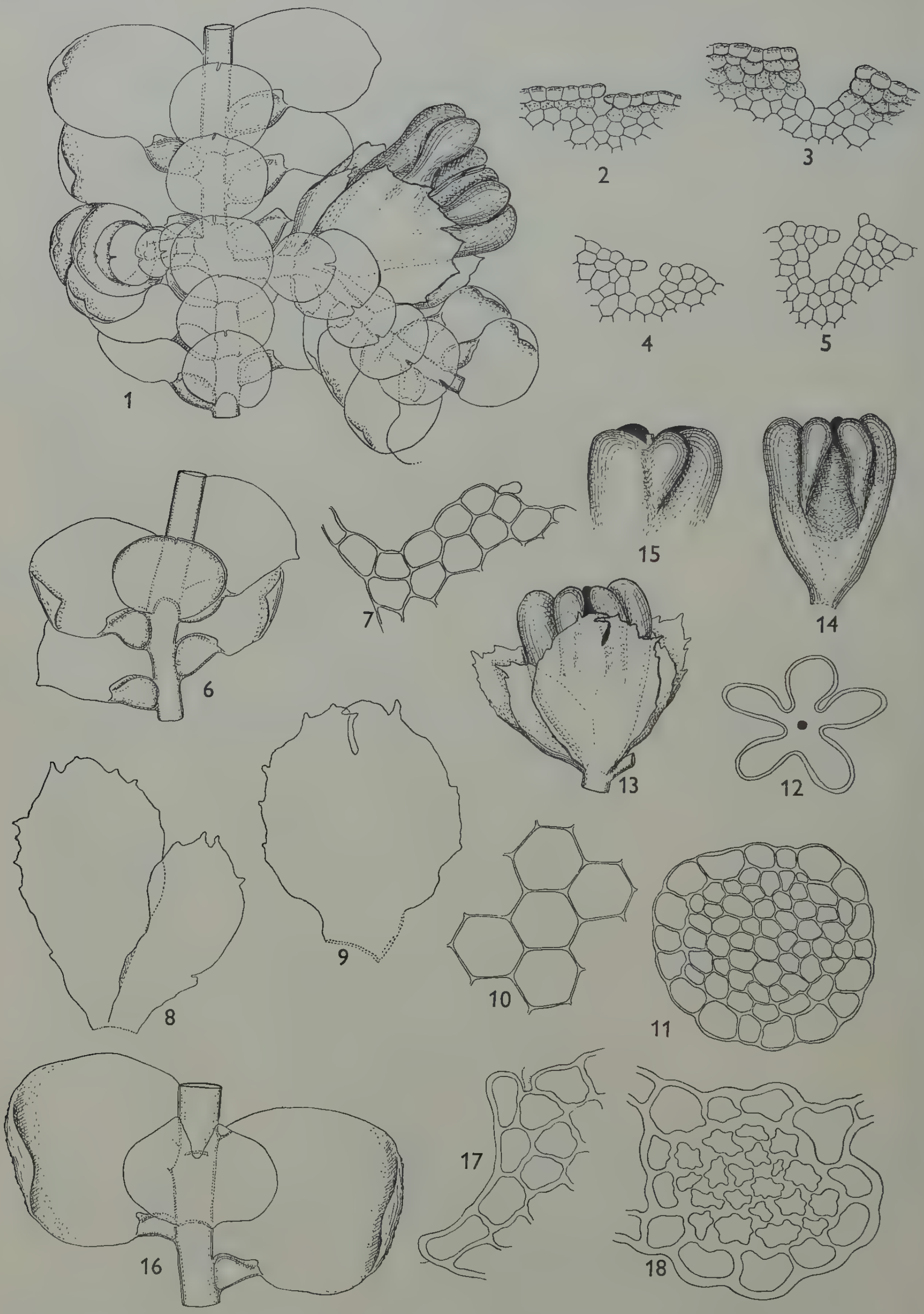


Fig. 7. *Pycnolejeunea (Perilejeunea) grandistipula* (Gottsche) St.: 1, plant with perianth, postical view (×20); 2–5, apices of underleaves (×80); 6, portion of shoot, postical view (×20); 7, apex of lobule (×190); 8, female bract (×30); 9, bracteole (×45); 10, leaf-cells (×325); 11, T.S. of stem (×125); 12, T.S. of perianth, near apex (×30); 13, perianth with bracts and bracteole, postical view (×17); 14, perianth, postical view (×17); 15, same, dorsal view, distal half only shown (×17). *P. (Pycnolejeunea) renistipula* (in Farlow herb.): 16, portion of shoot, postical view (×30); 17, apex of lobule (×250); 18, T.S. of stem (×170).

5. Lobule 'normal', opening towards the apex of lobe, orifice not very narrow, margined by 3–5 cells; stem with 7 rows of cortical cells; ventral merophytes 2 cells wide; cells with well-developed and coarse trigones, rarely with oval intermediate thickenings; median cells 22–25 μ wide. American. **7**

7. Ocelli present, few, scattered; underleaf 1·5 times as wide as long, 3–4 times as wide as stem. *P. spruceana* Schiffn.

7. Ocelli absent; underleaf twice as wide as long, 5–6 times as wide as stem. *P. papulosa* Steph.[1]

2. Lobuli strongly abbreviated, one-sixth to one-eighth the length of lobe; ocelli always present, few, scattered; cells more or less equally thickened, without distinct trigones; marginal cells 16–20 μ wide, median cells (19) 23–28 μ wide. Asian. **8**

8. Stem with 14 rows of cortical cells, the ventral merophytes 3–4 cells wide; ocelli large, $36\text{–}51 \times 75\text{–}95\,\mu$; underleaves 3·9 times as wide as stem, 1·5 times as wide as long, not auriculate at base. *P. sphaeroides* (Sde. Lac.) Steph.

8. Stem with 7 rows of cortical cells, the ventral merophytes 2 cells wide; ocelli when present small, $33\text{–}36 \times 39\text{–}45\,\mu$; underleaves about as long as wide; 4·2–5·5 times as wide as stem. **9**

9. Plants yellowish green when dry, rather large-sized, about 2·1 mm. wide; underleaves with a tendency to be auriculate at base; ocelli small, $33\text{–}36 \times 39\text{–}45\,\mu$; occasionally lobuli curved backwards, opening towards the posterior margin of lobe. *P. decurvifolia* Steph.

9. Plants dark-brown when dry, smaller, about 1 mm. wide; ocelli apparently absent or indistinguishable in dead material; underleaves somewhat truncate at base. *P. multiflora* Steph.

1. Lobuli large, one-half to three-quarters the length of lobe, apical tooth usually hardly projecting. **10**

10. Lobuli utriculate, strongly inflated throughout, 0·5 as wide as long; stem with 7 rows of cortical cells, ventral merophytes 2 cells wide; ocelli absent; underleaves distant to loosely imbricate; leaf-cells various. Asian. **11**

11. Leaf-cells large; marginal cells about 22 μ wide, median cells 29–33 μ wide, with coarse trigones and oblong-oval intermediate thickenings; trigones often subconfluent; cells with conspicuous middle lamellae; lobule 0·5–0·65 the length and 0·3 the width of lobe, the free margin involute from base to apex, the involute margin about 0·5 the width of lobule; apical tooth blunt, the cell immediately distad to the apical tooth large, at least twice the diameter of the adjacent cells; the posterior margin of lobe with a deep constriction, where it meets the apex of the keel, thus causing a separation of the lobular apex from the distal portion of lobe; leaves obovate; underleaves distant, about 2·9 times as wide as stem; plants 1·2 mm. wide, light yellowish brown when dry. *P. utriculata* Steph.

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[1] Spruce (1884, p. 248) mentions 'rarius ocellata' under *P.* '*contigua*' var. *latifolia*, but Stephani (1914, p. 604) does not mention ocelli under *P. papulosa* (= *P. contigua* var. *latifolia* and *P. pholidota* Spr. MS., vide Stephani; *Hedwigia*, **35** 126, 1895; *Spec. Hep.* 5, 604, 1914).

11. Leaf-cells small, marginal cells 14–16 μ wide, the median cells 17–20 μ wide, cells nearly equally thickened, trigones not distinct, without visible middle lamellae; lobuli 0·75–0·85 the length and 0·5 the width of lobe; the free margin reflexed from base to apex; apical tooth undefined; the posterior margin of lobe rather deeply convex, without a constriction where it meets the free margin of lobule; leaves ovate to subrotundate; underleaves 5·3 times as wide as stem, loosely imbricate; plants brown when dry, 0·9–1 mm. wide. *P. ventricosa* Schiffn.

10. Lobuli narrow, oblong to oblong-lingulate, inflated chiefly along the keel, 3–7 times as long as wide, sinus oblique or at about 90° to the posterior margin of lobe; stem anatomy various; cells with coarse trigones, the marginal cells 15–23 μ wide, median cells (22)24–34 μ wide; ocelli present, at least twice as long as wide; underleaves densely imbricate. **12**

12. Lobuli 3–4 times as long as wide; stem with 7–9 rows of cortical cells, the ventral merophytes 2 cells wide; underleaves 4 times as wide as stem; ocelli large, 45–60 × 80–95 μ. South-eastern Asia. *P. borneensis* Steph.

12. Lobuli 4–7 times as long as wide; stem anatomy various. American. **13**

13. Stem with the ventral merophytes 3–4 cells wide, the cortical cells in 13 rows; ocelli many, 45–99 × 30–48 μ; the posterior margin of lobe usually revolute, the keel straight; plants normally dioecious; underleaves as wide as long, 2·5–3 times as wide as stem. *P. schwaneckei* (Steph.) Schiffn.

13. Stem with the ventral merophytes 2 cells wide, the cortical cells in 7 or 10 rows; ocelli few. **14**

14. Stem with the cortical cells in 7 rows; ocelli large, 51–60 × 66–80 μ; underleaves as broad as wide, 2·5–3 times as wide as stem, sinus acute; posterior margin of lobe straight, without an indentation (but the keel convex); sinus of lobule rather oblique with respect to the posterior margin of lobe. *P. macroloba* (Mont.) Schiffn.

14. Stem with the cortical cells in 10 rows; ocelli 66–75 × 45 μ; underleaves 3–4 times as wide as stem, sinus broad; the posterior margin of lobe with a distinct indentation where it meets the free margin of lobule, the sinus at an angle of 85–90° with the free posterior margin of lobe. *P. callosa* (Ldbg.) Steph.[1]

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[1] *P. callosa* (Ldbg.) Steph. = *P. soleniloba* Spr. MS.; *Spec. Hep.* 5, 609, 1914.

Subgenus *Perilejeunea*[1] subg.n.

Pycnolejeunea Stephani, 1914, *Spec. Hep.* **5**, 611 (in part).

Plants delicate, moderately robust (about 1·6 mm. wide), in dense tufts, loosely appressed to substrate; when dry yellowish to yellowish green; profusely branched, branches irregularly pinnate, all branches of *Radula*-type; microphyllous shoots never developed. Stem pale, the cortical cells in 20–22 rows, the medullary cells in *ca.* 44–46 rows; the ventral merophytes *ca.* 6 cells wide; all cells thin-walled, the angles slightly to not thickened; the cortical cells 1–1·8 the diameter of the medullary. Leaves densely imbricate, widely spreading, the apex decurved. Lobe oblong-ovate, the antical margin rather strongly arcuate, base rounded to weakly rounded, extending beyond the axis, inserted on a long oblique line, apex apiculate, decurved; the margin entire, usually sinuate. Lobule obliquely rectangular, inserted on the axis nearly along its entire length, inflated along the weakly arched keel; the free margin incurved in the basal one-fourth only, the remainder of the free margin appressed to the lobe, bearing a single apical tooth; the apical tooth 1-cell long, blunt,[2] the hyaline papilla marginal, situated at the proximal base of the apical tooth; sinus oblique but truncate, ± continuous with the posterior margin of the lobe for a short distance. Leaf-cells thin-walled, rather plane, trigones minute, often indistinct; ocelli absent (at least in the material we examined). Underleaves strongly imbricate, large, 3·5 times as wide as stem, 1·75 times as wide as long, the apex and the lateral margins slightly deflexed, entire-margined; lobes variable, the underleaves often only slightly emarginate, occasionally with only a minute slit-like sinus, the lobes 1–3 cells long and 2–3 cells wide at base, rarely distinctly bilobed, the lobes then short, acute; underleaves inserted on a deeply arched line, the base strongly cordate. Asexual reproduction absent.

Gynoecia borne on short lateral leafy shoots, constantly with a single innovation, which may be again fertile. Bracts slightly smaller or as large as leaves, obliquely spreading, unequally bilobed, complicate; lobe oblong-obovate, broader in the distal half, margin dentate to denticulate; lobule 0·85 the length of lobe, oblong-obovate, dentate in the distal half, the keel with an indistinct short thin lamella. Bracteole adnate with one of the bracts at the base, ovate with an abruptly narrow base, margin dentate at apex, bifid; lobes acute to apiculate. Perianth obovate, terete, 5-plicate in the distal half, the plicae strongly inflated, dilated and produced as rounded crests distally; the short beak thus recessed; dorsal surface with a single plica. Androecia not seen (Fig. 7).

TYPE. *Pycnolejeunea grandistipula* G. ex Steph. The only species we know referable to the subgenus, our concepts being based on the plants in the Farlow Herbarium, from Caldas, Mineas Gaeras, Brazil (Mosen), det. Stephani. These plants are either topotypic or part of the type collection.

The subgenus *Perilejeunea* differs in a wide range of features from the subgenus *Pycnolejeunea*, as is evident from the foregoing key. Nevertheless, the leading features of the subgenus are typical of *Pycnolejeunea* s.lat.: for example, the dense leaves with deflexed apices; the dense, very large underleaves that are broader than long; the proximal hyaline papilla of the lobuli; the single innovations normally produced; the 5-carinate perianth; and the rather robust size.

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[1] Plantae tenues absque surculis microphyllis, pallide virides cum siccae sunt. Culmi holostipi, cellulis corticalibus in series 20–22 cellularum dispositis, merophytis ventralibus latis latitudine 6 cellularum. Foliorum apices apiculati, deflexi; lobulus oblique rectangularis, exigue inflatus ad carinam; cellulae foliorum tenuibus parietibus, planae, hexagonae, ut plurimum absque trigonis. Folia inferiora fortiter cordatae ad basim, marginibus atque apicibus reflexis. Gynoecia surculis brevibus lateralibus insidentia, constanter innovatione unica. Perianthium in sectione transversa teres, carinis quinque inflatis, atque supra dilatis, productis in cristas, rostro consequenter recedente. Bracteae atque bracteolae femineae dentatae.

Typus. *Pycnolejeunea grandistipula* G. ex Steph. (*Spec. Hep.* **5**, 611, 1914).

[2] One lobule was observed with the apical tooth 2 cells long.

DISTRIBUTION. We have not studied all of the species attributed to *Pycnolejeunea*. However, at least half of the species correctly referable to this genus stem from tropical America. The statements that the genus is well developed in south-east Asia, and elsewhere in the Old World tropics need re-investigation; part of the basis for such statements lies in earlier confusion with *Cheilolejeunea*.

REFERENCES. Spruce (1884–85); Evans (1906).[1]

ILLUSTRATIONS. *Pycnolejeunea schwaneckei* (Steph.) Schiffn.: Evans, 1906, *Bull. Torrey Bot. Cl.* **33**, 21–4, pl. 2, figs. 9–23; Stephani, 1888, *Hedwigia*, **27**, 289, pl. 13, fig. 28. *P. macroloba* (Mont.) Schiffn.: Evans, 1935, *loc. cit.*, **62**, 211, fig. 6, k.

TAXA WITH HYALINE PAPILLA DISTAL: *CHEILOLEJEUNEA* S. LAT.

The affinities of the majority of species discussed by Hoffmann (1935) under the name *Pycnolejeunea* are unquestionably with the taxa *Cheilolejeunea* and *Euosmolejeunea*. There has also been confusion with the genus or subgenus *Strepsilejeunea*, which differs from all other taxa here treated, and indeed from all others cited in the conspectus previously given, in the acute to bluntly pointed, deflexed apices of the leaves, and, typically, in the obsolete lobuli of the perichaetial bracts. In spite of this it is probable that *Strepsilejeunea* should be considered a mere subgenus of *Cheilolejeunea*. It need not be further discussed here, since its leading diagnostic features are adequately given in the conspectus.

The majority of species of *Pycnolejeunea* sensu Hoffmann are somewhat intermediate in their features between *Cheilolejeunea* and *Euosmolejeunea*. The latter two groups, commonly accepted as genera, have been recently united under the single genus *Cheilolejeunea* by Schuster (1955). The subgeneric name *Cheilolejeunea* was limited to the group of species with a 1-celled but long and acute to acuminate apical tooth of the lobule; these species apparently always have the perianth somewhat compressed and with a vestigial dorsal keel, or none at all; the underleaves in all cases were small and remote, averaging no more than twice as broad as the stem (Fig. 8). The subgenus *Euosmolejeunea* includes a much more variable series of species, which, however, agree in the following features: lobuli with apical tooth 1-celled, but the tooth formed of a blunt and little elongated, inconspicuous cell. The various species of *Euosmolejeunea* showed wide variation in the perianth keels, which ranged from 4 to 5, the dorsal being either sharp or obsolete; an equally great variability in underleaf size is found, the underleaves ranging from less than twice the stem width and remote from each other to 4–5 times the stem width and imbricate.[2]

Pycnolejeunea Hoffmann (pro max. parte), nec Spruce has the small underleaves traditionally attributed to *Cheilolejeunea*, but has apical teeth of the lobuli formed of little elongated cells, as is typical of *Euosmolejeunea*. The group shows, as does *Euosmolejeunea*, variation from 5-carinate and hardly compressed to 4-carinate and distinctly compressed perianths. However, the majority of species attributed to *Pycnolejeunea* by Hoffmann, and by other workers such as Jones, Herzog, and Hattori, differ from both *Euosmolejeunea* and *Cheilolejeunea* in three characteristics that we deem to be significant. These have been clearly brought out in our key on pages 476 and 477. For the species showing the ensemble of features enumerated therein we have selected the subgeneric name *Xenolejeunea* subg.n. since we find it strange that Hoffmann wholly failed to realize that the majority of

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[1] Schiffner (1893) and Stephani (1914) also treated *Pycnolejeunea*. Since they failed to distinguish this genus from *Cheilolejeunea*, *Siphonolejeunea*, *Nipponolejeunea* and *Tuyamaella*, their treatment has little value. Hoffmann (1935) on the east Asian species of *Pycnolejeunea* deals, in so far as we have been able to determine, with only a few species correctly referable to *Pycnolejeunea*.

[2] The original attempts at a separation of these two groups, *as genera* (or as subgenera of a portmanteau genus *Lejeunea*), as in Spruce (1884–85), Schiffner (1893), Evans (1906) are quite impossible to follow. Traditionally *Cheilolejeunea* was limited to species with a compressed, 4-carinate perianth and with small underleaves; *Euosmolejeunea* to species with a 5-carinate perianth and large underleaves. As Schuster & Hattori (1954) have shown, there are no significant differences between these two groups in oil-body form. The perianth character is totally without value as even a subgeneric criterion; equally ambiguous is the size of the underleaf, which varies widely in obviously related series of species. The only valid criterion to separate the two taxa appears to be that introduced by Schuster (1955), based on the form of the apical tooth of the lobule.

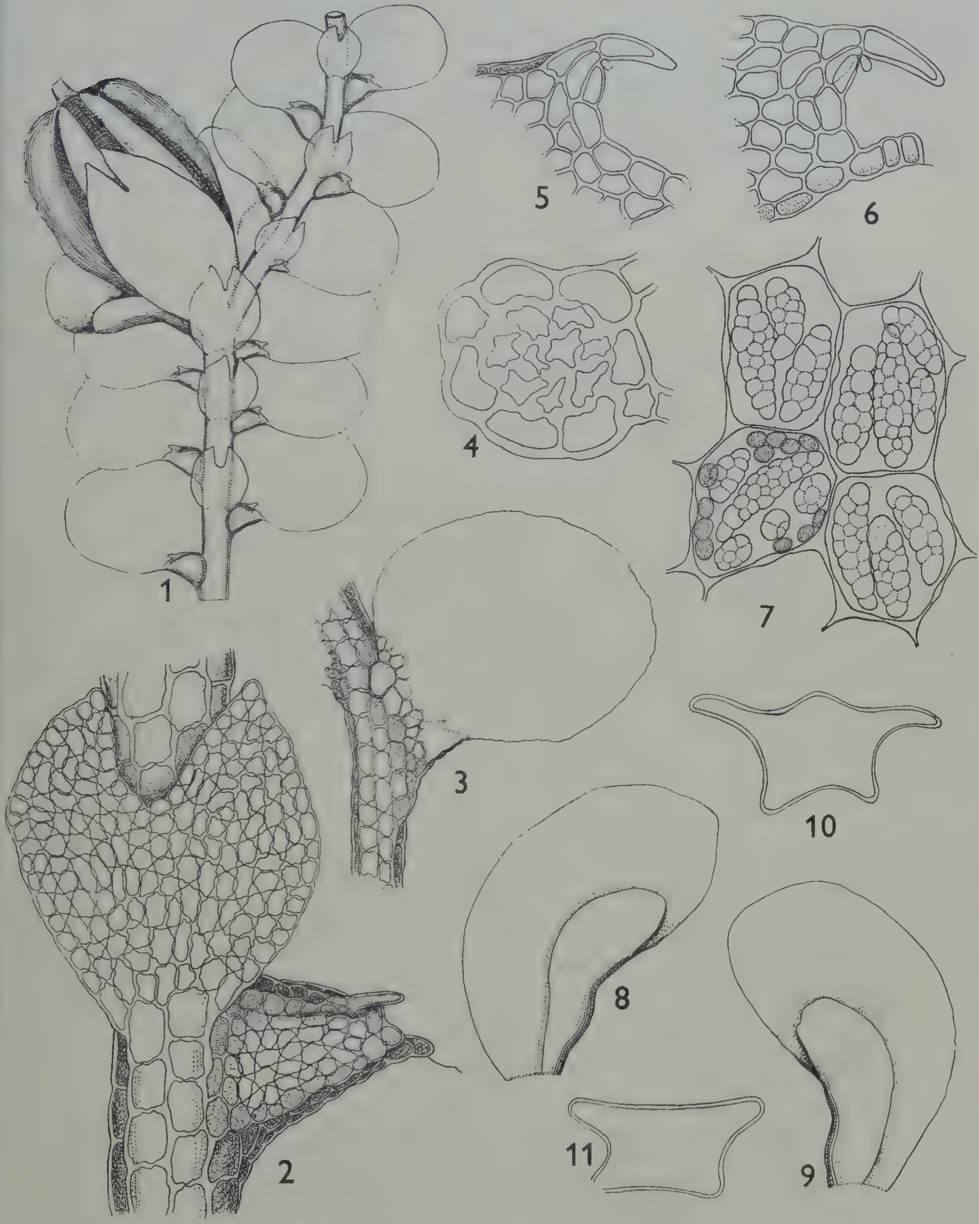

Fig. 8. *Cheilolejeunea aneogyna* (Spr.) Evans: 1, part of plant with perianth, postical view (×45); 2, part of shoot with underleaf and lobule, postical view (×215); 3, leaf, antical view (×107); 4, T.S. of stem (×412); 5, 6, apices of lobuli (×350); 7, median leaf cells with oil bodies (×412); 8, 9, female bracts (×72); 10, 11, cross-sections through middle of perianths (×67). (Fig. 8, 7 is drawn from *C. decidua* (Spr.) Evans, a species very similar to *C. aneogyna.*)

species attributed to his '*Pycnolejeunea*' were immediately allied to *Cheilolejeunea* and had not the remotest affinity to *Pycnolejeunea* (Spruce) Schiffn.[1]

Cheilolejeunea subgenus *Xenolejeunea* (*Pycnolejeunea* sensu Hoffmann, pro max. parte) is not a 'strong' subgenus. However, with the extraordinarily large number of species in the *Cheilolejeunea–Euosmolejeunea–Xenolejeunea–Strepsilejeunea* complex we are forced to utilize lesser characters as subgeneric characters. The weakness of the subgenus *Xenolejeunea* is evident when a series of species is studied that were referred by Hoffmann to *Pycnolejeunea*. (We specifically wish to eliminate from discussion here such species as *Pycnolejeunea angulistipa*, which is quite unrelated.) The species (of which we have seen material) with distal hyaline papillae of the lobuli referred to *Pycnolejeunea* by Hoffman fall into several groups, which can most readily be separated by the key following the subgeneric diagnosis (see also Table 2 on p. 500).

Subgenus *Xenolejeunea*[2] subg.n.

Pycnolejeunea Hoffmann, 1935. *Ann. Bryol.* **8**, 80–129; Stephani, 1914, *Spec. Hep.* **5**, 597 (in large part).

Plants medium sized to robust (1–2·1 mm. wide), forming depressed mats, usually prostrate, not glossy, rather profusely branched. Stem ± brown; the cortex and the ventral merophytes of a variable number of cell-rows; the cortex with 7–24 cell-rows, surrounding a medulla of 10–44 cell-rows, the ventral merophytes 2 or 4 cell-rows broad; either all cells equally thickened or similarly more or less thin-walled. Leaves loosely imbricate or not imbricate; lobe ovate-lingulate to oblong, rarely broadly ovate, somewhat convex, entire-margined; apex broadly rounded, not decurved; lobule variable in outline, typically narrow, elongate, 3·5 times as long as broad; keel nearly straight, rarely weakly convex; the apical tooth usually falcate, 2–4 or 6–7 cells long, sharply pointed, of ± isodiametric cells; the hyaline papilla distad of the apical tooth-margin, at the base of the apical tooth in a slight depression; sinus lunulate to nearly truncate. Underleaves distant, small, 1·5–3 times the stem-width, 0·4–0·65 (0·8) the length of lobe, nearly orbicular, bifid, 0·2–0·5 their length, lobes erect, triangular, acute; sinus acute; underleaves inserted on a slightly arched to nearly transverse line; base broadly cuneate, never auriculate or cordate. Leaf cells as in subg. *Cheilolejeunea*; ocelli absent.[3]

Gynoecia terminal on short or elongated shoots, with a single innovation. Bracts, bracteole and perianth varying as in *Cheilolejeunea*; dorsal keel usually low or obsolete;

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[1] Hoffmann nowhere mentioned *Cheilolejeunea* or *Euosmolejeunea*. He suggested that his *Pycnolejeunea*, which we have shown to be a *mélange* of unaffiliated elements, was allied to the holostipous genus *Leucolejeunea* Evans. It is ironic, perhaps, that there is a diffuse affinity between the groups of species which show the above ensemble of features (narrow lobuli; pluricellular apical tooth; narrow dorsal lobes) and *Leucolejeunea*, but that the basis for this putative relationship was quite misunderstood by Hoffmann. Hoffmann nowhere described the position of the hyaline lobular papilla in his *Pycnolejeunea*, even though he discourses, at length, as to the form of the lobule. Only at the end of his long paper did he imply that the lobule of his *Pycnolejeunea* (= *Cheilolejeunea*, pro max. parte) had a distal hyaline papilla, claiming that *Leucolejeunea* differed in having a proximal one. This is the feature which he presumed separated the two genera. However, both groups have a distal hyaline papilla! This possibly suggests a distinct relationship, as does the oil-body structure.

[2] Plantae medianae vel robustae; culmi cellulis corticalibus in series 16–24 dispositis, merophytis ventralibus latis latitudine 2 vel 4 cellularum. Folia laxe vel omino non imbricata, lobus terminalis late rotundatus, non recurvus; lobulus typice angustus, elongatus, 3·5 × longior quam latior, carina fere recta, raro exiliter convexus, dente apicali ut plurimum falcato, 2, 4, 6 vel 7 cellulis longo, acute acutuo, constanti cellulis plus minusve isodiametricis, papilla hyalina ad basim ulteriorem dentis apicalis in depressione. Folia inferiora distantia, parva, orbicularia, bifida, basis nec auriculata nec cordata. Cellulae foliorum ut in *Cheilolejeunea*; ocelli ut plurimum nulli. Gynoecia innovatione unica atque quoad alios characteres similia *Cheilolejeunea*. Androecia ut in *Cheilolejeunea*.

Typus. *Pycnolejeunea imbricata* (Nees) Steph.

[3] As far as studied by the authors. However, species like *P. grandiocellata* (Hoffmann *loc. cit.* p. 104, fig. 8) which appear to have a distal hyaline papilla, have ocelli.

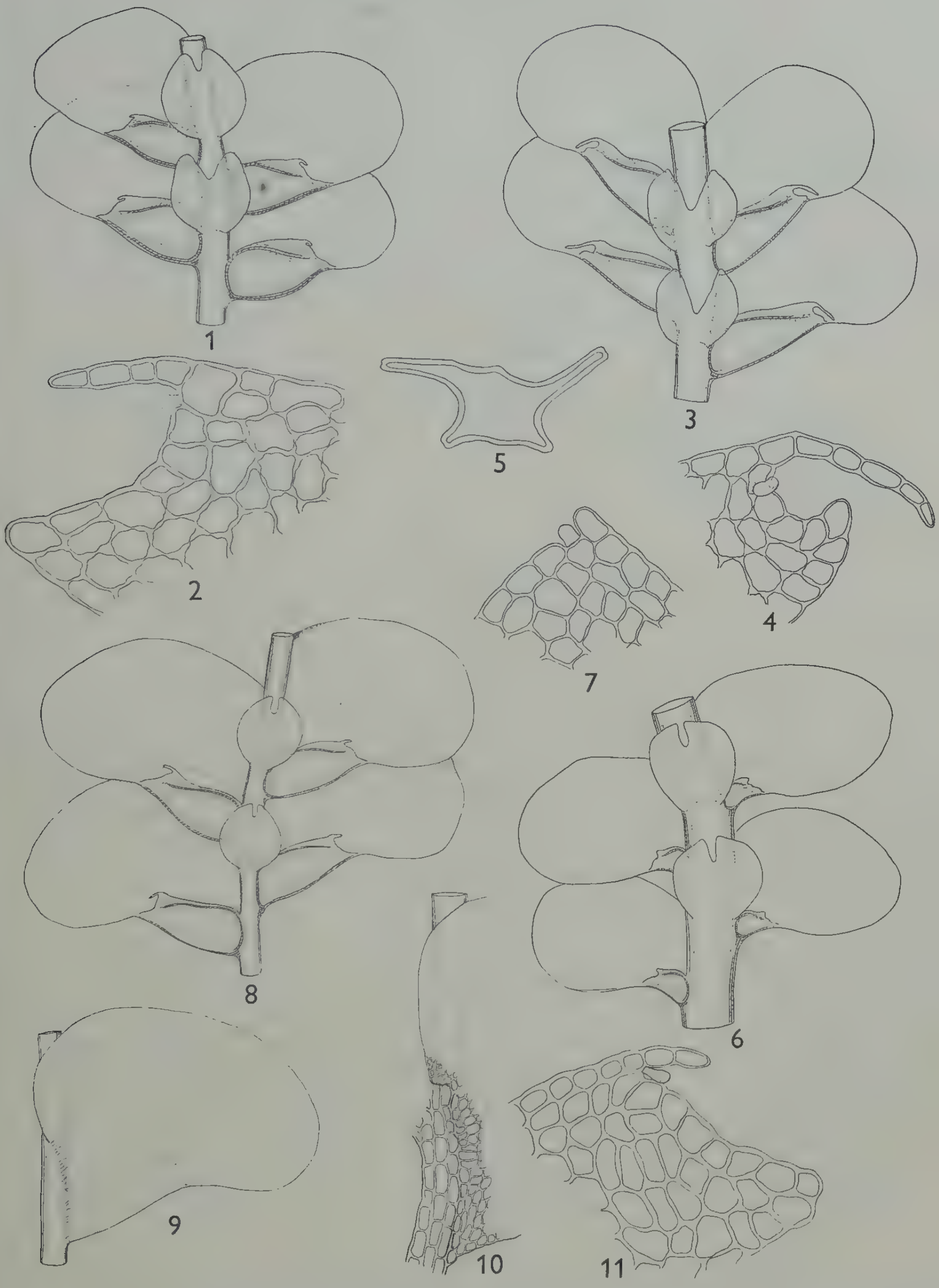

Fig. 9. *Cheilolejeunea* (*Xenolejeunea*) *tosana* (St.) Kachroo & Schuster: 1, part of shoot, postical view (× 50); 2, apex of lobule (× 412). *C.* (*X.*) *ceylanica* (Gottsche) Schuster & Kachroo: 3, part of shoot, postical view (× 55); 4, apex of lobule (× 412); 5, T.S. of perianth (× 62). *C.* (*X.*) *micholitzii* (St.) Kachroo & Schuster: 6, part of shoot, postical view (× 55); 7, apex of lobule (× 412). *C.* (*X.*) *meyeniana* (St.) Kachroo & Schuster: 8, part of shoot, postical view (× 47); 9, leaf, antical view (× 40); 10, insertion of lobe on axis, antical view (× 75); 11, apex of lobule (× 412). (In 2, 4, 7 and 11, note position of hyaline papilla.)

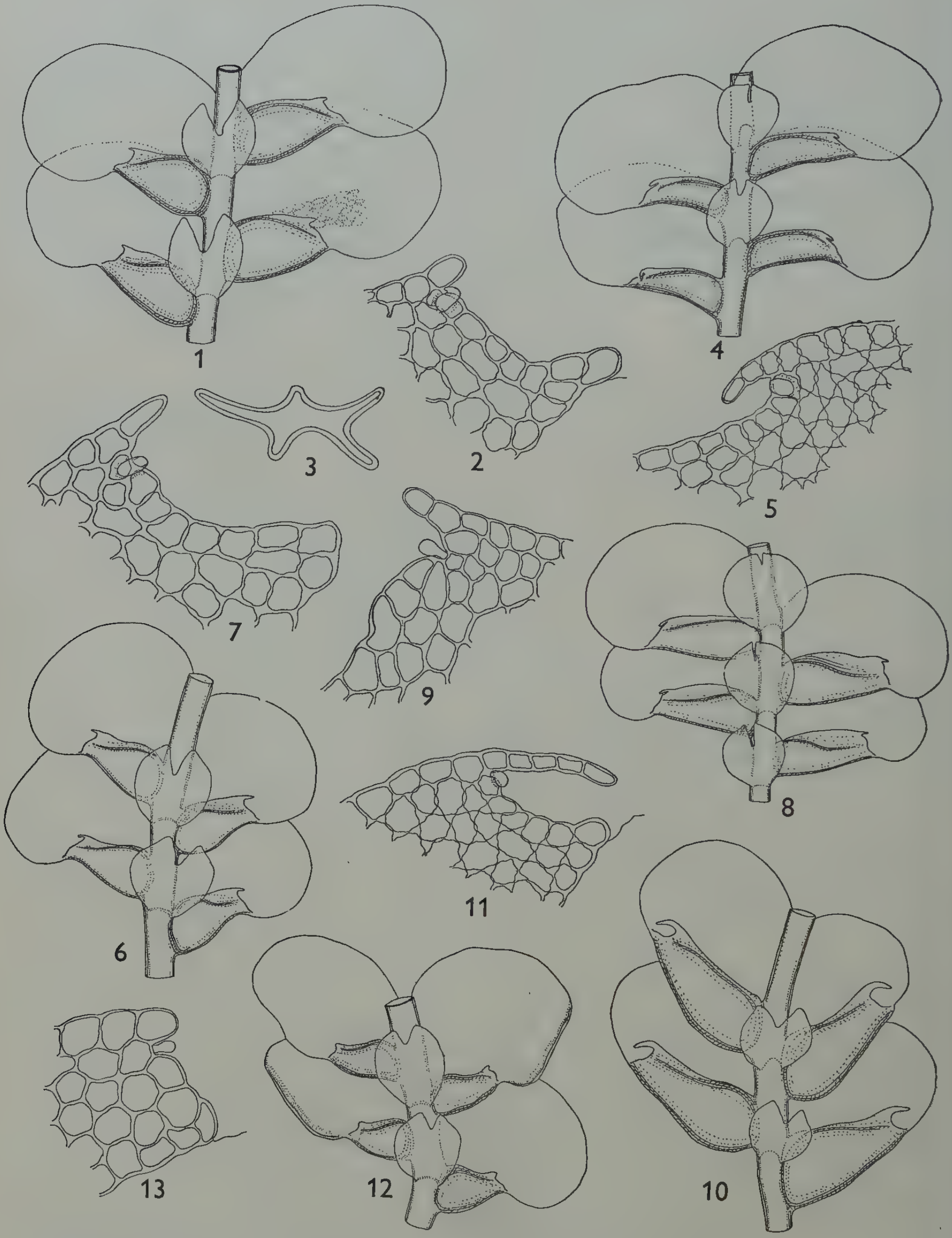

Fig. 10. *Cheilolejeunea* (*Xenolejeunea*) *vittata* (St.) Schuster & Kachroo: 1, part of shoot, postical view (×55); 2, apex of lobule (×412); 3, T.S. of perianth (×62). *C.* (*X.*) *longiloba* (St.) Kachroo & Schuster: 4, part of shoot, postical view (×47); 5, apex of lobule (×435). *C.* (*X.*) *incisa* (Gottsche) Schuster & Kachroo: 6, part of shoot, postical view (×55); 7, apex of lobule (×412). *C.* (*X.*) *trapezia* (Nees) Kachroo & Schuster: 8, part of shoot, postical view (×47); 9, apex of lobule (×412). *C.* (*X.*) *setifera* (St.) Schuster & Kachroo: 10, part of shoot, postical view (×67); 11, apex of lobule (×412). *C.* (*X.*) *discoidea* (L. et L.) Kachroo & Schuster: 12, part of shoot, postical view (×75); 13, apex of lobule (×412). (In 2, 5, 7, 9, 11 and 13, note position of hyaline papilla).

lateral and postical keels sharp or rounded, often variable on the same plant. Androecia as in *Cheilolejeunea*. (Figs. 3 (6–8), 4 (1–4), 6 (8–21), 9, 10).

TYPE. *Pycnolejeunea imbricata* (Nees) Steph.

Key to sections of Cheilolejeunea *subg.* Xenolejeunea

1. Lobular apical tooth 2–several cells long (and 1–2 cells broad at base), the hyaline papilla 2–7 cells from apex of lobule; lobuli always narrow and elongate, 0·5–0·85 the length of lobe. **2**

  2. Lobes narrowly oblong to ovate-oblong to obovate-oblong. **3**

    3. Stem with 18–24 rows of cortical cells that are thick-walled and slightly larger than medullary; ventral merophytes 4 cells broad; lobes widely spreading (75–85° usually); lobular apical tooth 2–3 cells long; keel long, nearly straight at an angle of 70–85°.
    (1.) Section Imbricatae (*C. imbricata*, *C. trapezia*)

    3. Stem with 7 (in *C. tosana* 10) rows of enlarged cortical cells, the ventral merophyte 2 cells broad; lobular apical tooth 3–7 cells long; keel usually at an angle of 55–70° (in *C. longiloba* 75–85°), usually somewhat convex.
    (2.) Section Ceylanicae (*C. ceylanica*, *C. tosana*, *C. meyeniana*, *C. longiloba*)

  2. Lobes broadly ovate, little or not longer than broad. **4**

    4. Apical tooth 2 cells long, straight; lobuli 0·6–0·65 length of lobes, normal in size; *ca.* 16 rows of cortical cells developed.
    (3.) Section Incisae (*C. incisa*)

    4. Apical tooth *ca.* 5 cells long, uniseriate throughout, long and falcate; lobuli 0·8–0·85 length of lobe, very large; stem with seven rows of cortical cells.
    (4.) Section Setiferae (*C. setifera*)

1. Lobular apical tooth 1- (rarely 2-)-celled, short and blunt; lobuli 0·5–0·2 length of lobe; lobe narrow, oblong-lingulate to oblong-rectangulate; stem with seven rows of cortical cells. **5**

    5. Lobuli larger, 0·5 length of lobe; lobe with a basal area of strongly elongated, enlarged cells. (5.) Section Vittatae (*C. vittata*)

    5. Lobuli very small, 0·2–0·5 the length of lobes; lobe without vitta.
    (6.) Section Discoideae (*C. micholitzii*, *C. discoidea*)

From inspection of the figures given, and the preceding key, it is clear that the position of the species placed in the last two sections is quite ambiguous: the 1-celled, blunt, apical tooth strongly suggests the subgenus *Euosmolejeunea*, in which, however, the leaves are usually more nearly rotundate! In fact, *C. micholitzii* (and the section to which it belongs) will surely have to be transferred to the subgenus *Euosmolejeunea*, even though it has no immediate relatives in that subgenus. With respect to the penultimate section, the Vittatae, a decision is much harder to make. As is clear from Fig. 10 (1), the narrow lobes strongly suggest *Xenolejeunea*, in spite of the *Euosmolejeunea*-like apical lobular tooth. The shape of the lobuli is rather broad for *Xenolejeunea*, but hardly broad enough for a typical species of *Euosmolejeunea*; this species may, therefore, be considered as intermediate. The dimorphic cells, with a basal vitta of ocelli developed, however, isolate *C. vittata* from all known species of *Euosmolejeunea* and *Cheilolejeunea*. It is possible that, after future study, this species and the other ocellate species referred to *Pycnolejeunea* by Hoffmann, will be removed to a separate subgenus. Since we do not have material of these ocellate species, except for *P. vittata*, it is impossible to clarify the confusion introduced by Hoffmann in this connexion. The ocellate species of *Pycnolejeunea* sensu Hoffmann are therefore best left in abeyance, as they surely do not belong to the *Euosmolejeunea–Cheilolejeunea* complex, and probably cannot be referred to *Xenolejeunea* either.

In addition to the great variability in the preceding series of characters, two other noteworthy features of the species of *Pycnolejeunea* sensu Hoffmann, with distal hyaline papillae, have been investigated, namely the perianth form and stem anatomy. The perianths are nearly equally variable as in *Euosmolejeunea*. Typically the antical perianth face is flat, or even concave (as, for example, in *C. imbricata*, Fig. 3 (8)); in other cases it bears a vestigial fifth keel (as, for example, in *C. ceylanica*, Fig. 9 (5)). However, *C. vittata*, a species that is deviant in other respects (such as in the vittate lobes), has a sharp dorsal carina of the perianth (Fig. 10 (3)). Further study of the perianths of the more typical species of *Xenolejeunea* (i.e. species of Sections 1–3) is needed.

Table 2. *A comparison of some primary characters of some species of* Cheilolejeunea *subgenus* Xenolejeunea

Species	Cortical cell-rows	Ventral merophytes in cell-rows	Lobule-type
C. incisa	16	3	Elongate-obovate, apical tooth 1-celled, acuminate
C. micholitzii	7–8	2	Small, obovate, apical tooth 1-celled, acuminate
C. cookiensis	7	2	Similar, apical tooth 2-celled
C. meyeniana	7	2	Narrow, elongate, apical tooth 2–3-celled
C. vittata	7	2	Broadly ovate to obovate, apical tooth 1-celled (or 2-celled on the same shoot)
C. longidens	7	2	Similar, apical tooth 1-celled
C. verdoornii	14–15	3–4	Similar, apical tooth 4–6-celled
C. discoidea	7	2	Broadly obovate, apical tooth 1-celled, blunt
C. longiloba	7	2	Narrow, elongate, apical tooth 2-celled
C. trapezia	18–24	4	Similar, apical tooth 2-celled
C. imbricata	22	4	Similar, apical tooth 2-celled
C. ceylanica	7	2	Similar, apical tooth 6-celled
C. tosana	10	2	Elongate-obovate, apical tooth 4-celled
C. setifera	7	2	Elongate, more or less narrow, apical tooth 4-celled
C. falsinervis	7–8	2	Similar, apical tooth 5-celled; a false median nerve in the lobe
C. gigantea	16–17	4	Large, obovate-ovate, 0·6–0·75 the length and 0·5–0·4 the width of lobe, dilated throughout, apical tooth undefined, blunt

Possibly more significant than the perianth form as a criterion is the stem anatomy (see Fig. 4). In several cases we found a correlation between species having an ensemble of the three characters we consider typical of *Xenolejeunea*, and a complex stem anatomy. These species (of Sections 1 and 3) showed a stem with 16–24 rows of cortical cells averaging only slightly, if at all, larger in diameter than the medullary cells (Fig. 4 (1, 2, 4)). Finding a stem anatomy of the type 'normal' for the Holostipae in this complex proved a great surprise, since in virtually all the hundred-odd species of Schizostipae investigated we had found a 'holostipous' stem anatomy only in *Potamolejeunea* and in some species of true *Pycnolejeunea*! Indeed, Schuster (1955) had emphasized the difference in stem anatomy as a subfamily character, stating the Holostipae normally had a stem with numerous (over 10) rows of cortical cells and the Schizostipae with usually 7 rows of enlarged cortical cells. At that time of writing only two or three isolated exceptions to this rule were known, and Evans (1935) in his important study of the stem anatomy of the Lejeuneaceae, found only one species of Schizostipae (*Potamolejeunea orinocensis*) with numerous rows of cortical stem cells.

We have investigated the species of both *Euosmolejeunea* and *Cheilolejeunea*, including the genotypes, and find they have the typical 'schizostipous' stem anatomy, i.e. 7 rows of large cortical cells. Having shown before that *Pycnolejeunea micholitzii* possesses the small lobuli, with a blunt, 1-celled apical tooth, of *Euosmolejeunea*, we were not surprised to find that the stem anatomy proved identical with that of the *Cheilolejeunea–Euosmolejeunea* complex (Fig. 9 (6, 7)). Similarly, the allied '*P.*' *discoidea*, and the isolated

'*P.*' *vittata*, both of which agree with *P. micholitzii* in having 1-celled lobular apical teeth and relatively small and short lobuli, possess a stem anatomy of the schizostipous type, i.e. with 7 rows of enlarged cortical cells. There is, therefore, an evident correlation between an *Euosmolejeunea*-like lobule and apical lobular tooth, and an *Euosmolejeunea*-like stem-anatomy with 7 rows of large cortical cells. Unfortunately, an inverse relationship does not hold. Although, for example, we found that several species with narrow, elongate lobuli and slender, pluricellular apical teeth (i.e. *C. incisa*, *C. trapezia* and *C. imbricata*) had a stem with 16–24 rows of cortical cells, and ventral merophytes 3–4 cells broad, others showed a simpler stem anatomy. *C. tosana* was intermediate, with 10 rows of cortical cells. The other species examined (*C. meyeniana*, *C. longiloba*, *C. setifera* and *C. ceylanica*) possessed a typical schizostipous stem anatomy, with 7 rows of cortical cells and ventral merophytes two cells broad. As a consequence we have been reluctantly forced to abandon the stem anatomy as a truly major criterion in this group; it is, at best, of sectional value. As has already been shown under *Pycnolejeunea* s.str., a distressingly similar variability in stem anatomy also occurs in that genus.

In view of the facts demonstrated above, the separation of the subgenus *Xenolejeunea* from the subgenera *Cheilolejeunea* and *Euosmolejeunea* cannot be readily effected in all cases. As with so many other technical groups, evaluation of an ensemble of features must be used. The more important of these are assembled in the preceding diagnosis.

TAXA WITH THE HYALINE PAPILLA ENTALLY DISPLACED: *NIPPONOLEJEUNEA*, *TUYAMAELLA* AND *SIPHONOLEJEUNEA*

The two segregates from *Pycnolejeunea* sensu Stephani, Schiffner and Hoffmann, which have the hyaline papilla entally displaced were described by Hattori (1944, 1947) as *Nipponolejeunea* and *Tuyamaella*. These genera show resemblances with each other in the following features, in addition to the papillar origin: a very narrow transverse insertion of lobe on the axis; the lobule strongly constricted at base, with two marginal teeth each at least 2 cells long; all branches of the *Radula*-type; ocelli absent. Even though sharing the above characters, these genera appear to be only remotely related to each other and probably deserve to be placed into two separate tribes or subfamilies.

Nipponolejeunea and *Tuyamaella* are, however, at least remotely related to *Siphonolejeunea* described by Herzog (1948). Since *Nipponolejeunea*, *Tuyamaella* and *Siphonolejeunea* have not been critically investigated they deserve special treatment here.

(*a*) *Nipponolejeunea* Hattori (Figs. 11, 12) is based on '*Pycnolejeunea*' *pilifera* Steph. It differs from *Pycnolejeunea* s.str. in the narrow insertion of the lobe and lobule on the axis; the lobule with two pluricellular marginal teeth; in the entally displaced hyaline papilla, the subrotundate underleaves, very slightly emarginate at apex; the leaves in part with long, marginal cilia; the absence of ocelli; the leaf-cells without coarse trigones; the sharply trigonous compressed perianth; the gynoecial bracteole free; and in the bracts with a strongly convex, tectate keel. *Nipponolejeunea* further possesses the following characters: the stem without hyalodermis, its anatomy typically holostipous, the cortical cells lying in 24 rows, the medullary cells in about 26 rows, the ventral merophytes 4–several cells wide; oil-bodies more or less granular, usually 3–4 (5–7) per cell; the gynoecia on leading shoots, with 1–2 subfloral innovations; and the seta of the capsule with 16 peripheral cell-rows, surrounding the four central cell-rows.

Nipponolejeunea is in some respects probably one of the most primitive members of the Lejeuneaceae. It was placed formerly in the Schizostipae, but it does not bear any close affinities to that subfamily. However, *Nipponolejeunea* shares several critical features with the primitive members of the Holostipae: a similar stem anatomy, the trigonous, compressed perianth, and the seta of the sporophyte with 16 peripheral cell-rows. The ability to produce marginal cilia of the leaves is unique.

(*b*) *Tuyamaella* Hattori (Figs. 13, 14), based on '*Pycnolejeunea*' *molischii* Schiffner

(Schiffner, 1929), differs from *Pycnolejeunea* s.str. in the narrow insertion of lobe and lobule on the axis; the lobule with two marginal teeth, each 2–3 cells long; the entally displaced hyaline papilla; in asexual reproduction by means of discoid gemmae of the surface of the leaf lobes; in the absence of ocelli; and in the coarse trigones of the leaf cells. *Tuyamaella* shows further the following significant characteristics: the stem anatomy schizostipous, the cortical cells in 7 rows, at least twice the diameter of the medullary, the latter in 3 rows, the ventral merophytes in 2 cell-rows; leaves without cilia; gynoecia on

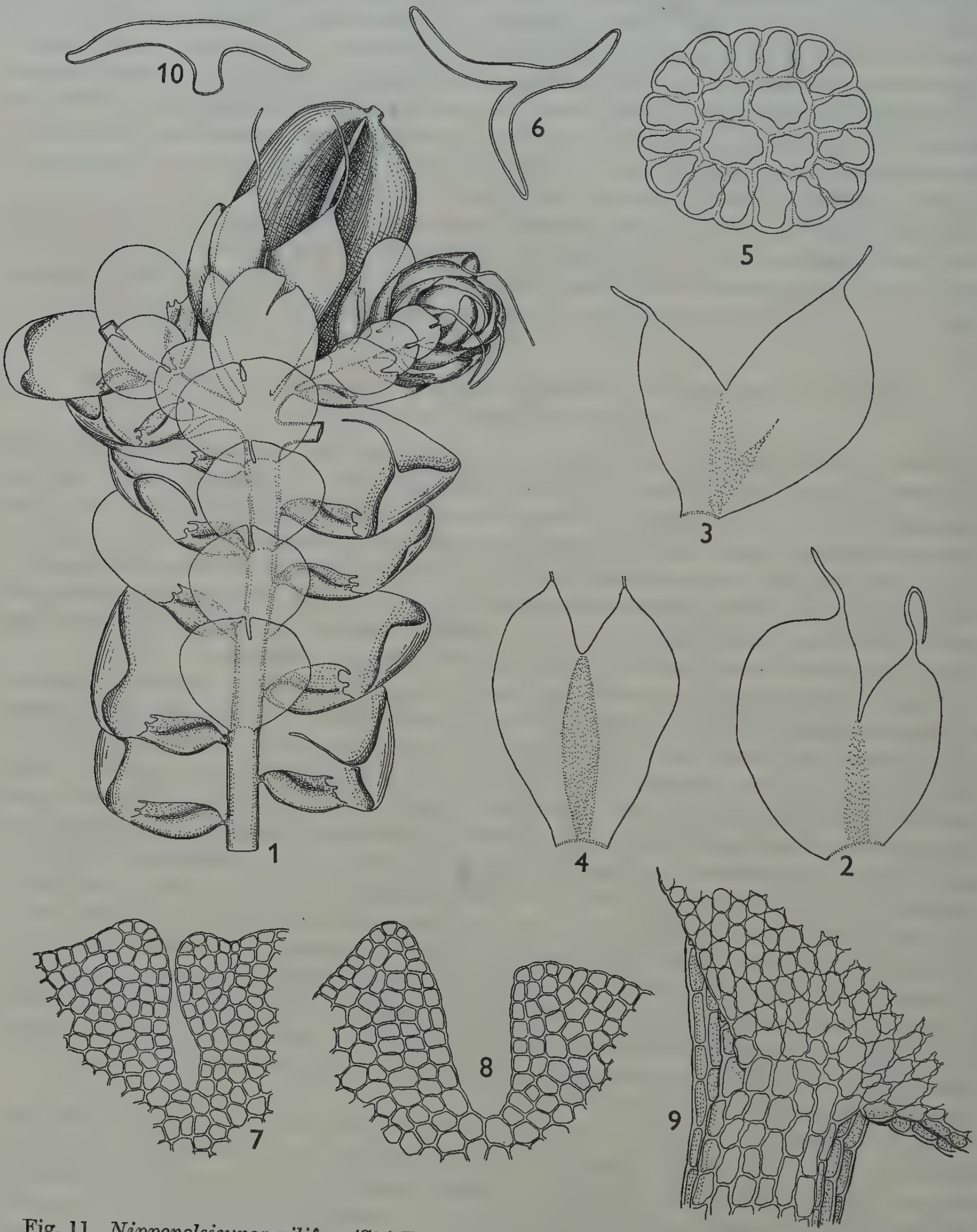

Fig. 11. *Nipponolejeunea pilifera* (St.) Hattori: 1, plant with perianth, postical view (×27); 2, 3, female bracts (×35); 4, bracteole (×35); 5, T.S. of seta (×125); 6, T.S. of perianth, near apex (×42); 7, 8, apices of underleaves ×180; 9, base of lobe showing insertion on the axis, ×15; 10, t.s. perianth, ×18.

long or short shoots, always with a single innovation; perianth 5-carinate, not strongly compressed, the dorsal keel single, often low or obsolete; the gynoecial bracteole adnate to one of the bracts at base; oil-bodies compound, granular, 3–6 (7–8) per cell in the leaf-middle, up to 20 per cell in the basal cells.

Tuyamaella has a number of features in common with both the Schizostipae and the Paradoxae. It resembles the Schizostipae in having twice as many lateral leaves as underleaves, but the entire facies of the genus recalls to a great extent *Diplasiolejeunea*.

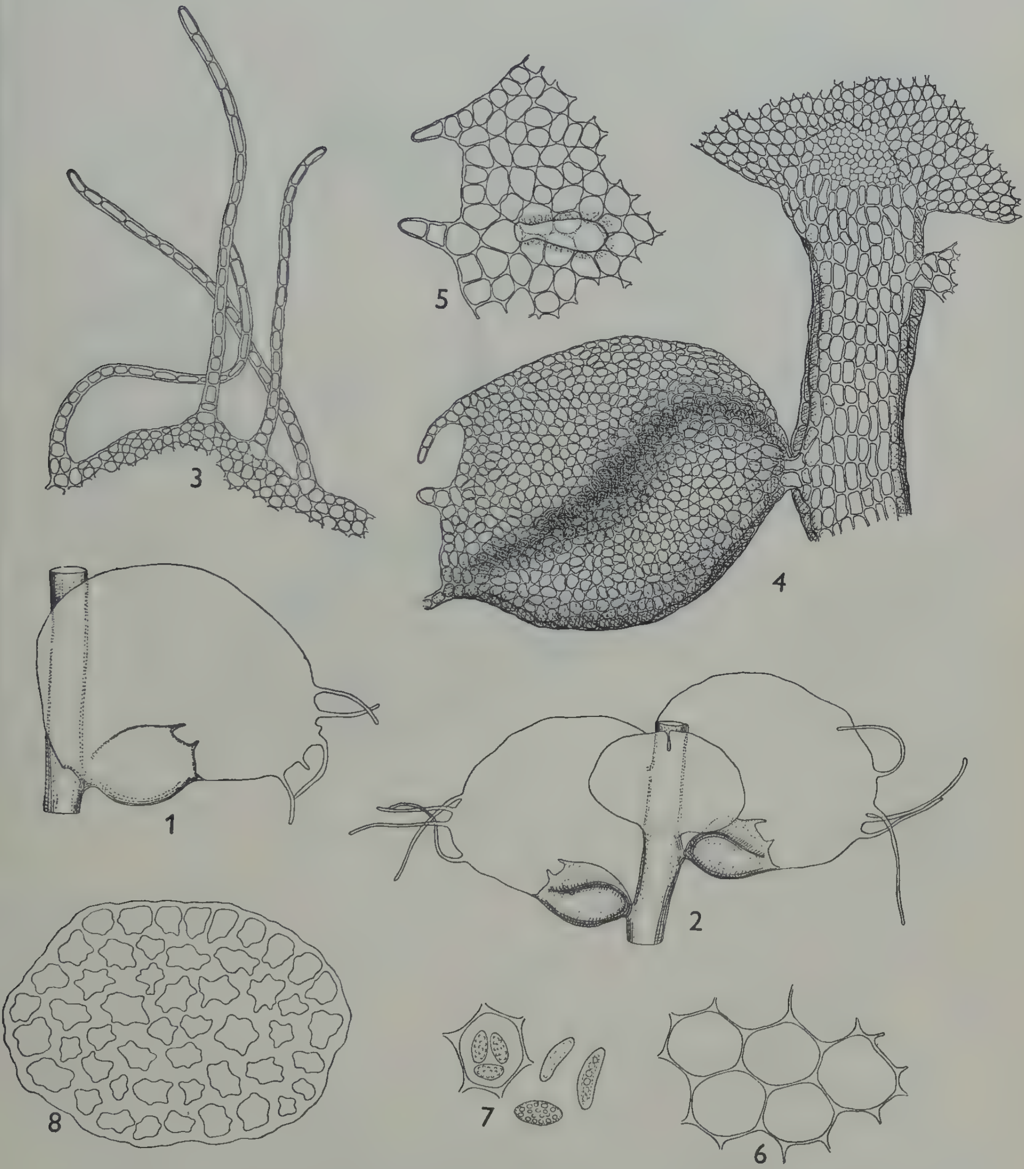

Fig. 12. *Nipponolejeunea pilifera* (St.) Hattori: 1, portion of shoot, antical view (× 37); 2, same, postical view (× 37); 3, apex of leaf showing filiform cilia (× 120); 4, portion of shoot, postical view, showing insertion of underleaf, ventral merophytes and lobule (× 100); 5, apex of lobule showing apical tooth and hyaline papilla (× 223); 6, leaf cells (× 412); 7, leaf cell with oil-bodies and individual oil-bodies (× 412, 500); 8, T.S. of stem (× 325).

Tuyamaella resembles *Diplasiolejeunea* in the abbreviated insertion of the lobule on the stem, the similar apical tooth, the 5-carinate, somewhat compressed perianth, the bilobed underleaves, with divaricate lobes, in the border of hyaline, dead cells of leaves, in the

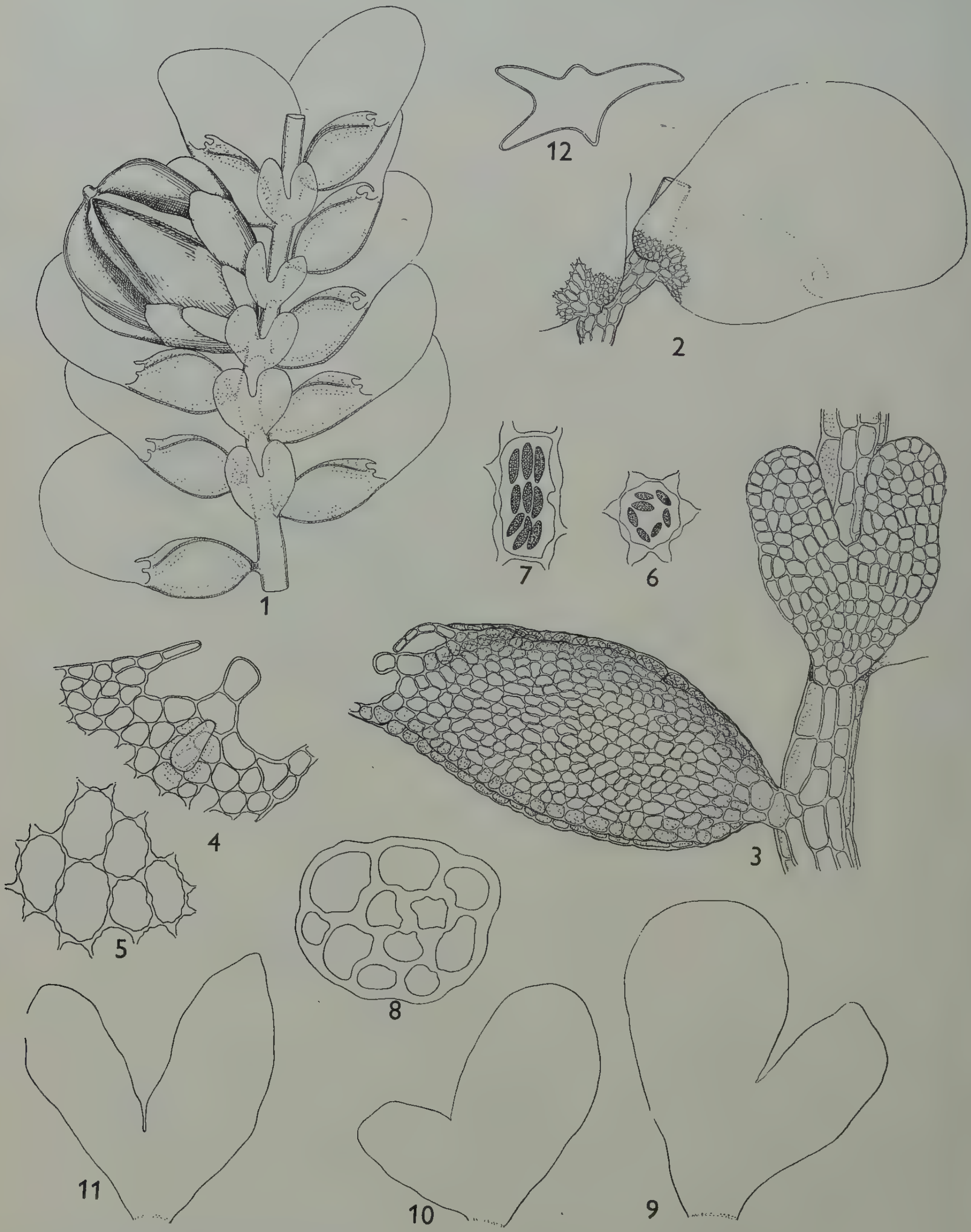

Fig. 13. *Tuyamaella molischii* (Schiffn.) Hattori: 1, plant with perianth, postical view (× 42); 2, portion of shoot, antical view, showing insertion of leaf with the axis (× 62); 3, same, postical view, showing insertion of underleaf and that of lobule (× 155); 4, apex of lobule showing apical tooth and hyaline papilla (× 242); 5, leaf cells (× 412); 6, same (median) with oil-bodies (× 412); 7, same (basal) with oil-bodies (× 275); 8, T.S. of stem (× 412); 9, 10, female bracts (× 130); 11, bracteole (× 130); 12, T.S. of perianth, near apex (× 67).

discoid gemmae of leaf surfaces, in the gynoecial bracteole adnate with one of the bracts at base. The only major characters separating the two genera are in the number of underleaves and in the cytology.[1] *Tuyamaella* thus appears to be more immediately related to the Paradoxae, rather than to the Schizostipae, under which it has been previously treated. However, the lack of duplication of the underleaves signifies a very low position with respect to other genera of the Paradoxae and it may be advisable to place this genus in a separate subfamily.

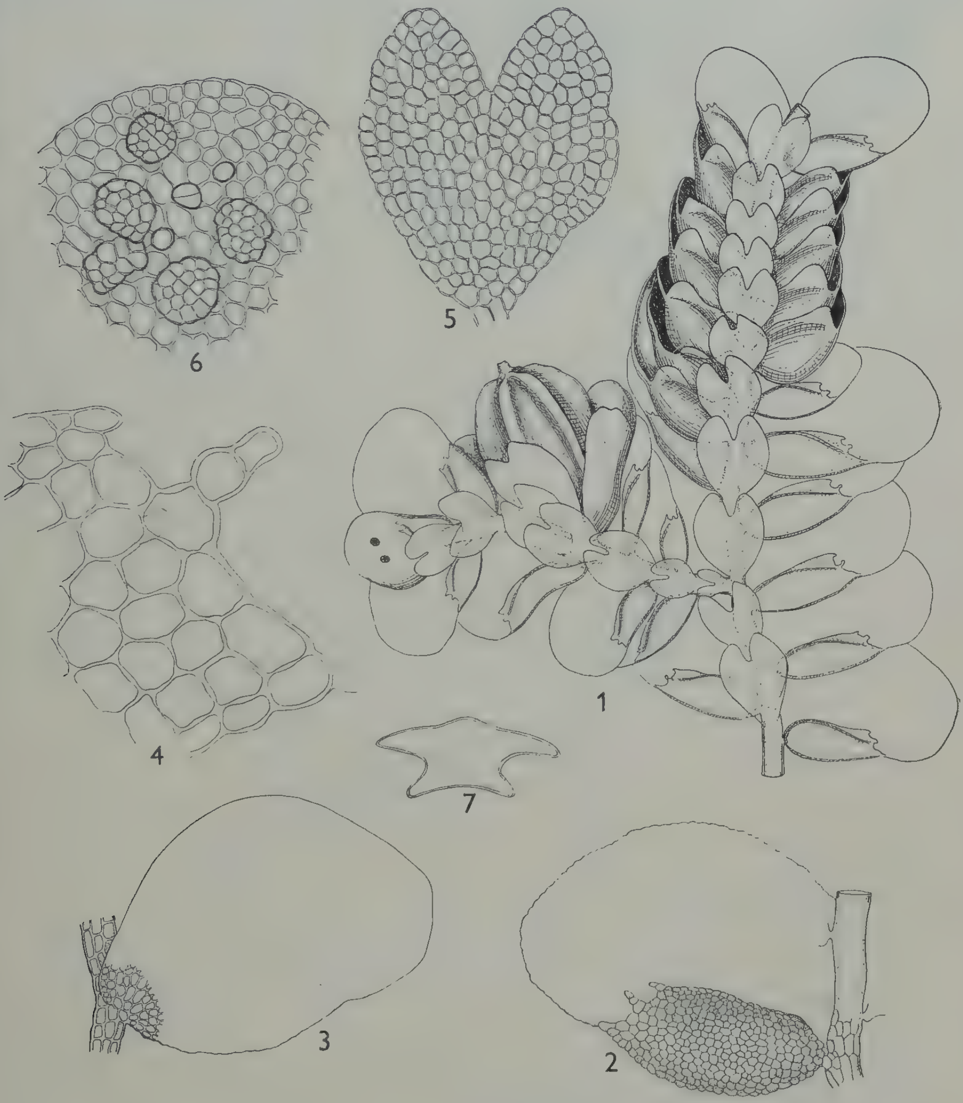

Fig. 14. *Tuyamaella angulistipa* (St.) Schuster & Kachroo: 1, plant with androecium and gynoecium (× 30); 2, portion of shoot, postical view, showing insertion of lobule to the axis (× 62); 3, same, antical view, showing insertion of lobe with the axis (× 62); 4, apex of lobule showing apical teeth and entally displaced hyaline papilla (× 412); 5, underleaf (× 120); 6, portion of apical region of leaf, showing dorsal gemmae (× 150); 7, T.S. of perianth, near apex (× 25).

[1] For a treatment of the oil-bodies and ocelli of *Diplasiolejeunea* see Schuster & Hattori (1954).

(c) *Siphonolejeunea* Herzog (Figs. 15, 16) is based on '*Pycnolejeunea*' *schiffneri* Steph. *in lit.*, *Siphonolejeunea nudicalycina* Herz. and *S. nudipes* (Tayl.) Herz. It has a characteristic slender, tubularly involute lobule with an obscure, undefined, single apical tooth. We consider such a lobular structure as reduced from that of the *Tuyamaella*-type of

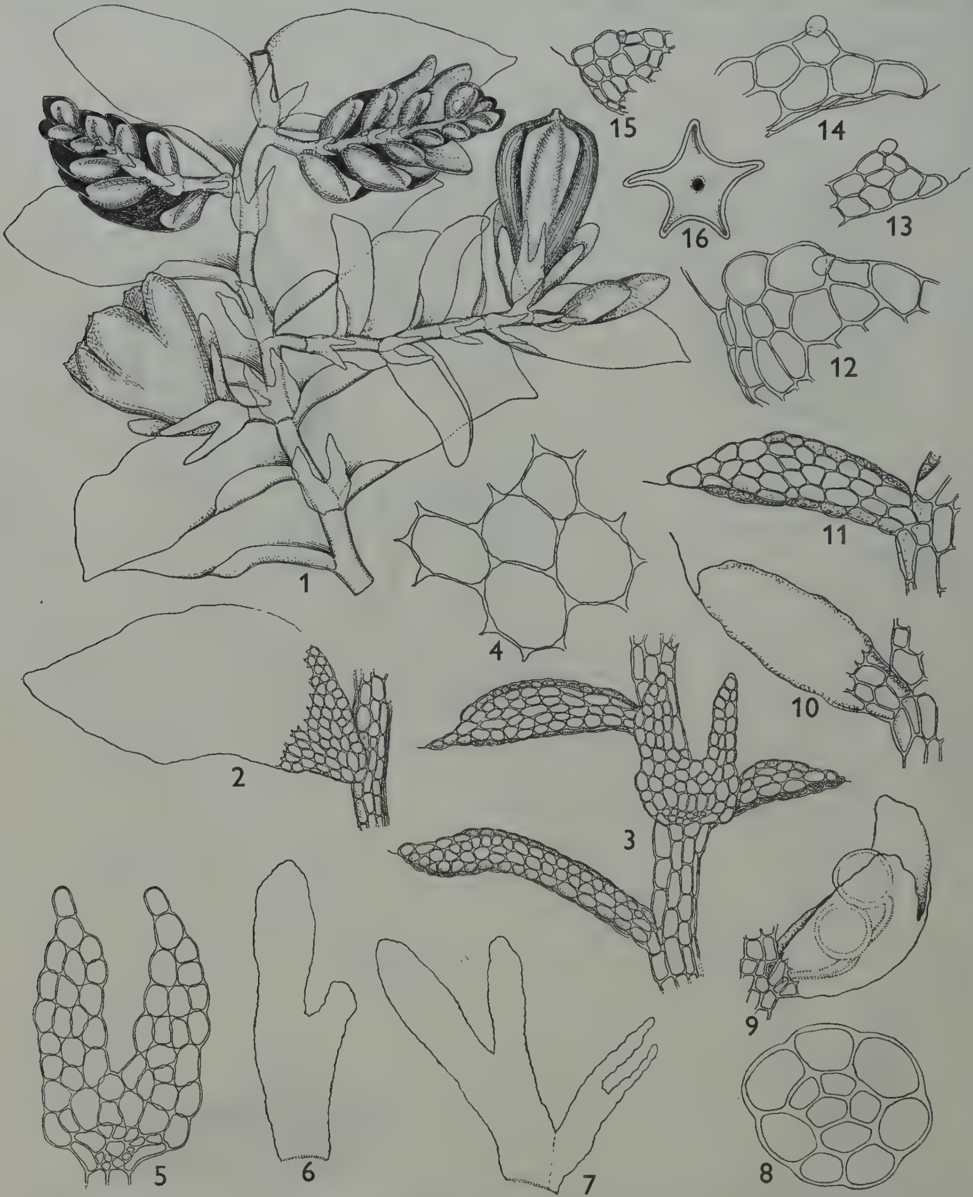

Fig. 15. *Siphonolejeunea nudicalycina* Herzog: 1, plant with androecia and gynoecia, postical view (× 57); 2, portion of shoot, showing the narrow insertion of lobe on axis (× 62); 3, same, showing insertion of lobuli on the axis and an underleaf (× 62); 4, leaf-cells (× 375); 5, underleaf (× 162); 6, female bract (× 75); 7, same, with bracteole, adnate at base (× 75); 8, T.S. of stem (× 375); 9, male bract, diandrous (also showing narrow insertion of lobule) (× 112); 10, 11, lobuli, showing narrow insertion on axis and (11) undefined apical tooth (× 112); 12–15, apices of lobuli, each showing undefined apical tooth and hyaline papilla (12, 14 × 285); (13, 15 × 135); (12, 14, × 285; 13, 15, × 135); 16, t.s. apex of perianth (× 57).

lobule, the two salient marginal teeth of that genus having been lost; in consequence the hyaline papilla is situated on the undefined apical tooth, the latter is represented by the slightly protruding terminal cell of the lobule, occasionally hardly differentiated from the surrounding cells. *Siphonolejeunea* differs further from *Pycnolejeunea* in: narrowly obovate-lingulate to lanceolate-lingulate leaves, acute or rounded at apex; both lobe and lobule narrowly inserted on the axis; underleaves bifid near to base, with lanceolate, erect to weakly divergent, acute to pointed lobes; discoid gemmae of the leaf lobes; absence of ocelli; and absence of coarse trigones of leaf-cells. The other primary distinguishing features of *Siphonolejeunea* are: the gynoecia on long or short leafy shoots, with single subfloral innovation; the perianth 5-plicate in the distal 0·5–0·7, not compressed; the gynoecial bracteole adnate with one of the bracts at the base; androecia terminal on short lateral shoots, without bracteoles distally; stem schizostipous, with 7 rows of cortical cells, the medullary cells in *ca.* 5 rows and the ventral merophytes 2 cells wide.

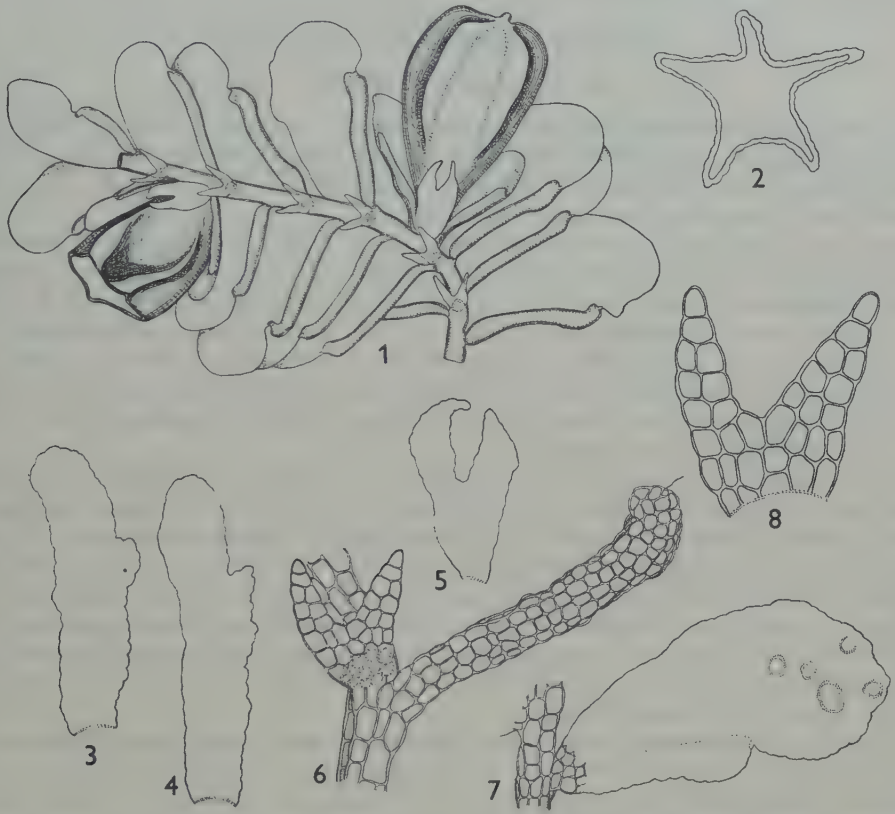

Fig. 16. *Siphonolejeunea schiffnerii* (St. in sched.) Herzog: 1, plant with perianths (× 32); 2, T.S. of perianth, near apex (× 57); 3, 4, female bracts (× 62); 5, bracteole (× 80); 6, underleaf and lobule (× 112); 7; 8, underleaf (base not shown) (× 212), portion of shoot, antical view showing insertion of lobe on axis, and gemmae (× 75).

From the ensemble of characters enumerated above, it is evident that *Siphonolejeunea* is closely allied to *Tuyamaella*. The two genera have a similar stem anatomy, similar discoid gemmae of the leaf lobes; bifid underleaves, with erect to suberect, occasionally slightly divergent lobes; a 5-carinate perianth that is not to somewhat compressed; single subfloral innovations; the bracteole adnate with one of the bracts at base; and lack ocelli.

The preceding brief discussion of these three genera, i.e. *Tuyamaella*, *Nipponolejeunea* and *Siphonolejeunea* has shown that no affinity of these genera to *Pycnolejeunea*, however broadly conceived, can be postulated. The nature of the leaf-insertion, the form of the lobule, and position of the hyaline papilla, the nature of the asexual reproduction (unknown to date only in *Nipponolejeunea*), the absence of ocelli, the nature of the leaf-cells, and a series of other features suggest that these three genera bear closer affinities to the Paradoxae, and, perhaps, in the case of *Nipponolejeunea*, to the Holostipae, than they do to the schizostipous genus *Pycnolejeunea*. Surely the confusion which has existed in this connexion reflects only the largely superficial work which has been done on the group, rather than any real relationship.

PERTINENT TRANSFERS AND SYNONYMY

(1) To *Tuyamaella* Hattori

1. *Pycnolejeunea molischii* Schiffner, in *Ann. Bryol.* **2**, 97, figs. 7–8, 1929; Horikawa, *Bot. Mag., Tokyo*, **46**, 177, 1932; Horikawa, *J. Sci. Hiroshima Univ.* Ser. B, Div. 2, **2**, 272, 1934; Kamimura, *J. Jap. Bot.* **15**, 73, 1939; Horikawa, *J. Jap. Bot.* **15**, 397, 1939; Hattori, *Bull. Tokyo Sci. Mus.* no. 11, 127, 1944.

Pycnolejeunea boninensis Horikawa, *loc. cit.* 1, 25, pl. 2, figs. 1–11, 1931 = *Tuyamaella molischii* (Schiffn.) Hattori, *Bull. Sci. Mus., Tokyo*, **15**, 76, 1944 (nomen nudum); Hattori, *Biosphaera*, **1** (1), 3, 1947; Hattori, *J. Hattori. Bot. Lab.* no. 5, 62, fig. 41, 1951.

2. *Pycnolejeunea appendiculata* Herzog, *Mem. Soc. F. Fl. Fennica*, **26** (1949–50), 62, figs. 37, 38*e*, 1951 = *Tuyamaella appendiculata* (Herz.) Schuster & Kachroo, comb.n.

3. *Pycnolejeunea angulistipa* Steph., *Hedwigia*, **35**, 123, 1896; Stephani, *Spec. Hep.* **5**, 632, 1914; Hoffmann, *Ann. Bryol.* **8**, 108, fig. 9*a–b*, 1935 = *Tuyamaella angulistipa* (Steph.) Schuster & Kachroo, comb n.

We have studied *P. angulistipa* from material determined by Hoffmann, issued in Verdoorn's Hep. Select. & Crit. No. 437 (from eastern Java). The plants represent a typical species of *Tuyamaella*, and bear no relationship to *Pycnolejeunea* at all. The leaf insertion is typical of *Tuyamaella*, with both lobes and lobuli constricted at base and very narrowly attached to the stem; the lobes bear dorsal discoid gemmae; the underleaves are bifid, and the stem has seven rows of cortical cells; the lobuli are elongate and bear two teeth distally, with the hyaline papilla entally displaced and situated on the inner base of the apical tooth, which is 3-celled; the cells are hexagonal, with the walls somewhat thickened but with no large trigones.

The species differs from the other two species of *Tuyamaella* which we have studied, in: (*a*) the underleaf is widest medially, with the lobes narrowly rounded to blunt, but not broadly truncate, and not divergent; the sinus is acutish; (*b*) the bracteole resembles the underleaves and is not deeply bifid.

(2) To *Nipponolejeunea* Hattori

1. *Pycnolejeunea pilifera* Steph. ex Inoue, *Bot. Mag., Tokyo*, **14**, 39, 1900 (nomen nudum); Yoshinaga, *Bot. Mag., Tokyo*, **20**, 53, 1906 (nomen nudum); Stephani, *Spec. Hep.* **5**, 624, 1914; Horikawa, *J. Sci. Hiroshima Univ.* Ser. B, Div. 2, **1**, 130, pl. 16, 1932; Horikawa, *ibid.* **2**, 272, 1934; Horikawa, *in* Asahina, *Nippon Inkwasyokubutu Dukan*, p. 863, pl. 414, figs. 1–13, 1939.

Dicranolejeunea japonica Steph., *Spec. Hep.* **6**, 386, 1923 = *Nipponolejeunea pilifera* (Steph.) Hattori, *Bull. Tokyo Sci. Mus.* no. 11, 125, fig. 76, 1944; Hattori, *Bull. Hattori Bot. Lab.* no. 8, 35, 1952.

2. *Pycnolejeunea subalpina* Horikawa, *J. Jap. Bot.* **15**, 360, figs. 13–14, 1939 = *Nipponolejeunea subalpina* (Horik.) Hattori, *Bull. Tokyo Sci. Mus.* no. 11, 125, 1944; Hattori, *J. Hattori Bot. Lab.* no. 8, 35, 1952.

(3) To *Cheilolejeunea* subgenus *Xenolejeunea* subg.n.

1. *Pycnolejeunea okamurana* Steph., in Yoshinaga, *Bot. Mag., Tokyo*, **20**, 54, 1906 (nomen nudum); Stephani, *Spec. Hep.* **5**, 627, 1914; Hattori, *Bull. Tokyo Sci. Mus.* no. **11**, 127, fig. 77, 1944.

Pycnolejeunea imbricata (Nees) Steph., *Bull. Herb. Boissier*, **5**, 80, 1897; Schiffner, *Consp. Hep. Archip. Ind.* p. 258, 1898; Hoffmann, *Ann. Bryol.* **8**, 98, fig. 7*a*, 1935; Hattori, *J. Hattori Bot. Lab.* **5**, 55, fig. 37, 1951.

Lejeunea imbricata Nees, in G. L. & N., *Syn. Hep.*, p. 359, 1845 = *Cheilolejeunea* (*Xenolejeunea*) *imbricata* (Nees) Schuster & Kachroo, comb.n.

2. *Pycnolejeunea vittata* (Steph., in Sched.) Hoffmann, *Ann. Bryol.* **8**, 115–16, fig. 9*c*, *d*, 1935 = *Cheilolejeunea* (*Xenolejeunea*) *vittata* (Steph.) Schuster & Kachroo, comb.n.

3. *Pycnolejeunea incisa* (Gottsche) Steph., *Spec. Hep.* **5**, 624, 1914, *Lejeunea incisa* Gottsche, *Syn. Hep.*, p. 360, 1845 = *Cheilolejeunea* (*Xenolejeunea*) *incisa* (Gottsche) Schuster & Kachroo, comb.n.

4. *Pycnolejeunea trapezia* (Nees) Steph., *Spec. Hep.* **5**, 625, 1914. *Lejeunea trapezia* Nees, *Syn. Hep.*, p. 357, 1845 = *Cheilolejeunea* (*Xenolejeunea*) *trapezia* (Nees) Kachroo & Schuster, comb.n.

5. *Pycnolejeunea setifera* Steph., *Spec. Hep.* **5**, 626, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *setifera* (Steph.) Schuster & Kachroo, comb.n.

6. *Pycnolejeunea discoidea* (L. et L.) Steph., *Spec. Hep.* **5**, 612, 1914. *Lejeunea discoidea* L. et L., *Syn. Hep.*, p. 383, 1845 = *Cheilolejeunea* (*Xenolejeunea*) *discoidea* (L. et L.) Kachroo & Schuster, comb.n.

7. *Pycnolejeunea ceylanica* (G.) Steph., *Spec. Hep.* **5**, 621, 1914. *Lejeunea ceylanica* Gottsche, *Syn. Hep.*, p. 359, 1845 (= *L. connivens* G., in Schiffner, *Gazellen Exped.*, 1889) = *Cheilolejeunea* (*Xenolejeunea*) *ceylanica* (Gottsche) Schuster & Kachroo, comb.n.

8. *Pycnolejeunea micholitzii* Steph., *Spec. Hep.* **5**, 627, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *micholitzii* (Steph.) Kachroo & Schuster, comb.n.

9. *Pycnolejeunea cookiensis* Steph., *Spec. Hep.* **5**, 617, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *cookiensis* (Steph.) Schuster & Kachroo, comb.n.

10. *Pycnolejeunea falsinervis* Steph., *Spec. Hep.* **5**, 622, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *falsinervis* (Steph.) Kachroo & Schuster, comb.n.

11. *Pycnolejeunea gigantea* Steph., *Spec. Hep.* **5**, 630, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *gigantea* (Steph.) Schuster & Kachroo, comb.n.

12. *Pycnolejeunea verdoornii* Hoffmann, *Ann. Bryol.* **8**, 118, fig. 12*a–c*, 1935 = *Cheilolejeunea* (*Xenolejeunea*) *verdoornii* (Hoffmann) Kachroo & Schuster, comb.n.

13. *Pycnolejeunea longidens* Steph., *Spec. Hep.* **5**, 634, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *longidens* (Steph.) Schuster & Kachroo, comb.n.

14. *Pycnolejeunea tosana*[1] Steph., *Spec. Hep.* **5**, 626, 1914 = *Cheilolejeunea* (*Xenolejeunea*) *tosana* (Steph.) Kachroo & Schuster, comb.n.

15. *Pycnolejeunea meyeniana* (G., Ldbg. et Nees) Steph., *Spec. Hep.* **5**, 628, 1914. *Lejeunea meyeniana* G. L. et N., *Nova Acta Acad. N. Cur.*, **19**, 472 = *Cheilolejeunea* (*Xenolejeunea*) *meyeniana* (G. L. et N.) Schuster & Kachroo, comb.n.

16. *Pycnolejeunea longiloba* Steph. = *Cheilolejeunea* (*Xenolejeunea*) *longiloba* (Steph.) Kachroo & Schuster, comb.n.

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[1] Hattori (1951) regards *Pycnolejeunea tosana* as synonymous with *P. imbricata*. This investigation brings forth differences in the stem anatomy and lobular form between the two species and therefore we regard them as separate species (cf. Table 2).

(4) To *Pycnolejeunea* s.str.

Herzog[1] in his various papers appears to have inverted the characters of *Pycnolejeunea* and *Strepsilejeunea*, at least to the extent of referring species that appear to be *Pycnolejeunea* to *Strepsilejeunea*.

1. *Strepsilejeunea subcrenulata* Herz., *Ark. Bot.*, **29** A, 11, fig. 3*f–m*, 1940 = *Pycnolejeunea subcrenulata* (Herz.) Schuster & Kachroo, comb.n.

MATERIALS EXAMINED

The figures of the various species discussed in this paper were drawn from the following specimens, the source of the material follows the specific names and those marked with an asterisk are from the types:

Pycnolejeunea: *P. spruceana*,* Herb. A. W. Evans (Ex Herb. Gottsche); *P. macroloba*, Herb. Evans, no. 506; *P. papulosa*, Hep. Spruceanae: Amazon. et And. (as *P. contigua* var. *latifolia*); *P. soleniloba*, Hep. Spruceanae: Amazon. et And.; *P. schwaneckei*, Jamaica, Herb. Evans, no. 99; *P. decurviloba*, Herb. Evans, no. 7877; *P. malaccensis*,* Herb. Verdoorn, Arch., no. 21015; *P. multiflora*,* Herb. Verdoorn, Arch., no. 10996; *P. novoguineensis*,* Herb. Verdoorn, Arch., no. 11005; *P. sphaeroides*,* Herb. Verdoorn, Hep., no. 10192; *P. utriculata*,* Bryotheca Levier (Ex Farlow Herb.); *P. ventricosa*, Herb. Verdoorn, Arch., no. 21105; *P. bidentula*, Herb. Verdoorn, Arch., no. 10926,* 10932; *P. borneensis*,* Herb. Verdoorn, Hep., no. 10924; *P. decurvifolia*,* Herb. Verdoorn, Hep., no. 10942; *P. grandistipula*, Ex Farlow Herb.; *P. renistipula*,[3] Herb. Jack, ex Farlow Herb.; *P. deuissa*,[3] Gazellen Expedition, ex Farlow Herb.

Cheilolejeunea subg. Xenolejeunea: *C. verdoornii*,* Herb. Verdoorn, Arch., no. 15687; *C. cookiensis*, Bryotheca Levier, ex Farlow Herb. (co-type); *C. falsinervis*, Herb. Verdoorn, Hep., no. 10193; *C. gigantea*,* Herb. Verdoorn, Hep., no. 10935; *C. micholitzii*, Hep. Select. et Crit. Verdoorn, no. 411; *C. incisa*, Hep. Japan, Faurie, no. 1325; *C. imbricata*, Hep. Select. et Crit. Verdoorn, no. 439; *C. trapezia*, Mosses of Japan, Herb. Okamura; *C. discoidea*,* Herb. Mitten, ex NYBG; *C. longiloba*,[3] Flora Philippines, no. 10568; *C. setifera*, Flora Philippines, no. 6253; Herb. Verdoorn, Arch., no. 10901;* *C. tosana*, Hep. Japan; Faurie no. 695; *C. ceylanica*, Hep. Select. et Crit. Verdoorn, no. 438; *C. meyeniana*, Hep. Select. et Crit. Verdoorn, no. 440; *C. vittata*, Herb. Verdoorn, Hep., no. 2845 (type?), Hep. Select. et Crit. Verdoorn, no. 442; *C. longidens*, Herb. Levier, ex Farlow Herb.

Nipponolejeunea: *N. pilifera*, Hep. Japan, Hattori, no. 142; Hattori Bot. Lab., no. 14825; Hep. Japan, Faurie, nos. 1441, 1403.

Tuyamaella: *T. molischii*, Hep. Japan, Hattori, no. 300; *T. angulistipa*, Hep. Select. et Crit. Verdoorn, no. 437.

Siphonolejeunea: *S. nudicalycina*, Svenska Pacific expeditionen, 1916–17: Hep., no. 103 p.p., 104; ex NYBG; *S. schiffnerii*, Schiffner, no. 1449 p.p., ex Farlow Herb.

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[1] The following examples illustrate Herzog's occasional misunderstanding of the genus *Strepsilejeunea*:

(i) *Harpalejeunea verrucosa* Herz., *Mem. Soc. F. Fl. Fennica*, **25** (1948–49), 64, fig. 14, 1950 = *Strepsilejeunea verrucosa* (Herz.) Schuster & Kachroo, comb.n.

(ii) *Euosmolejeunea papillata* Herz., *Ark. Bot.*, Ser. 2, **3**, 57, fig. 7*a*–f, 1953 = *Strepsilejeunea papillata* (Herz.) Schuster & Kachroo, comb.n.

[2] As far as we know these species have not been described so far, nor are they included in Stephani's *Spec. Hep.* However, on the specimen packets (examined by us) their authorship is credited to Stephani!

SUMMARY

Pycnolejeunea, in recent years, has become an admixture of species belonging to diverse genera: *Nipponolejeunea*, *Tuyamaella*, *Cheilolejeunea*, *Siphonolejeunea* and *Strepsilejeunea*. Its history, delimitation and affinities, at times remote, to these genera, have been discussed. An analysis of the various species of '*Pycnolejeunea*' recently monographed by Hoffmann (1935) shows that the large majority of these species do not belong to *Pycnolejeunea*, but demonstrate unmistakable affinities with *Cheilolejeunea* emend. Schuster (1955); these species have been accordingly transferred to *Cheilolejeunea*, under subgenus nov. *Xenolejeunea*. Both *Pycnolejeunea* s.str. and *Cheilolejeunea* subg. *Xenolejeunea* show remarkable variation in their stem anatomy and the form and structure of lobule, and this has necessitated their division into several sections; such variation within each genus is discussed.

A similar study of the remaining species of '*Pycnolejeunea*' sensu Stephani et Hoffmann is desirable.

We are grateful to Dr J. R. Reeder (Herbarium Yale University) and the Farlow Herbarium for loaning us their entire collection of *Pycnolejeunea*; to Dr S. Hattori for sending specimens of *Nipponolejeunea* and *Tuyamaella* for our examination. Thanks are due to Mrs R. M. Schuster for her help in preparation of this paper, and to Rev. Dr H. Santapau for the Latin translations.

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The type species of *Bifurcaria* Stackhouse—a Correction

By R. ROSS, F.L.S.

Since the publication of my previous note on this subject (in *J. Linn. Soc. Lond., Bot.*, **55**: 753–4, 1958) Dr P. S. Dixon has drawn my attention to the fact that *Fucus bifurcatus* Velley (in Withering, *Bot. Arrang. Brit. Pl.* ed. 2, **3**: 257, 1792) is a later homonym of both *Fucus bifurcatus* Gunnerus (*Flor. Norveg.* **1**: 96, 1766) and *Fucus bifurcatus* Burman f. (*Flor. Cap. Prodr.*: [32], (ut '28'), 1768).

Fucus bifurcatus Gunnerus is treated by Agardh (*Spec. Alg.* **1**: 114, 1820) as a synonym of *Laminaria bulbosa* (Huds.) Lam., now generally known as *Saccorhiza polyschides* (Lightf.) Batt. Kützing (*Spec. Alg.*: 577, 1849) treats it as a variety of the North Pacific *Hafgygia bongardiana* (Post. & Rupr.) Kütz., which Setchell & Gardiner (in *Univ. Calif. Publ. Bot.* **8**: 605, 1925) refer to *Laminaria platymeris* Pyl. However, Foslie (in *Christiana Vid.-Selsk. Forhandl.* **1884** (14): 61, 1884) lists *Fucus bifurcatus* Gunn. among the synonyms of *Laminaria digitata* (Huds.) Lam. f. *debilipes* Foslie, and he saw Gunnerus's type.

The original publication of *Fucus bifurcatus* Burman in his list of the plants collected by Oldenland at the Cape of Good Hope reads: '——[Fucus] (bifurcatus) *Moris. hist.* 3. *s.*15. *t.*8. *f.*12'. The reference is to *Fucus palmaris angustifolius ad extrema vesiculosis rugosis bifurcatus* Morison (*Plant. Hist. Univ. Oxon.* **3**, sect. 15: 647, tab. 8 fig. 12, 1699) and the name is thus validly published and typified by Morison's description and figure. Dr E. F. Warburg has kindly examined the specimen in the Morisonian Herbarium on which these are based, and confirms the statement of Vines & Druce (*Account Morisonian Herb.*: 226, 1914) that it is *Pelvetia canaliculata* (L.) Dec. & Thur. (= *Fucus canaliculatus* L., *Syst. Nat.* ed. 12, **2**: 716, 1767). As this species is confined to the northern hemisphere, Burman must have been in error in identifying with Morison's figure the Oldenland specimen from the Cape on which he based this record.

It would appear that the name of the type species of *Bifurcaria* is not affected by the existence of these earlier homonyms. No other epithet that has been legitimately published and that can be applied to this species can be traced, and hence *Bifurcaria bifurcata* Ross is a legitimate name under Art. 72, Note, of the current (1956) edition of the *International Code of Botanical Nomenclature*, and the correct one for the species, but its epithet, like the name as a whole, only has priority from 1958 and '(Velley)' should not be included in the authority. The type, however, remains the specimen of *Fucus bifurcatus* Velley in his herbarium at the Liverpool Public Museum.